

Morgan L Vis  
Orlando Necchi Jr

# Freshwater Red Algae

Phylogeny, Taxonomy and  
Biogeography

 Springer

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*We dedicate this book to our phycological mentors Robert G. Sheath and Shigeru Kumano. They have served as an inspiration to our studies of freshwater red algae, and we would hope this book would meet with their approval.*

*We are grateful to our families, Wayne and Kyle Chiasson and Vânia, Lisandra, and Cauê Necchi. They have continuously supported us with their patience and sacrifice. Without them, we could never have done the research and written this book that we consider the masterpiece of our careers.*

# Preface

Since Linnaeus (1753) first described *Conferva gelatinosa*, the iconic freshwater red alga *Batrachospermum gelatinosum* (L) DC, researcher have been adding to our knowledge of the diversity for this important group of algae. In the nineteenth and twentieth centuries, treatises and regional floras provided new understanding of their classification. More recently, Shigeru Kumano's monograph *Freshwater red algae of the world* (2002) compiled all freshwater red algae in a single volume. In the 20 years following this publication, new methods, particularly DNA sequence data coupled with reassessment of morphological characters has transformed our understanding of the diversity of freshwater red algae requiring a new synthesis of this charismatic group.

This book presents modern, up-to-date, comprehensive information on the taxonomy, phylogeny, and biogeography of freshwater red algae worldwide. Chapter 1 includes a brief history of freshwater red algal studies, an overview of the diversity and phylogeny, biogeographic trends, how to collect and preserve, and finally the scope and organization of the book. Chapters 2–5 are divided into large taxonomic groups with freshwater representative. Each chapter provides summarized information on general characteristics for the higher ranks (subphyla to families), descriptions of genera and species including diagnostic characters, habitat, world distribution, and phylogenetic relationships among species and key to species. For each species, valuable data including type specimen and locality, illustrations (mostly photomicrographs), diagnostic characters, distribution, representative DNA sequences in GenBank, and key references are presented.

The book content has been designed to be a handy, easy-to-use, single source reference for a wide audience. For readers just starting to explore this group, there is background information as well as descriptions of genera and distribution maps. For those readers who are familiar with these organisms, there are details about type specimens, DNA sequence data, and comprehensive descriptions for each species.

The taxonomic keys and habitat information will allow professionals in several fields such as limnology, aquatic biology, water quality biomonitoring, and related areas the identification and environmental characterization of their materials.

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# Chapter 1

## History of Freshwater Red Algal Studies; Taxonomic Diversity and Phylogeny; Biogeographic Trends; Collection of Freshwater Red Algae; Scope and Organization of This Book



Orlando Necchi Jr and Morgan L Vis

**Abstract** A brief history of freshwater red algal studies is provided with a focus on researchers who wrote early treatises on cryptogams, those who pioneered studies focused on freshwater red algal taxonomy, research on freshwater red algae in several parts of the world and studies that applied new types of evidence for systematics research. Our current knowledge of the taxonomic diversity of freshwater red algae and their phylogenetic relationships is summarized. The biogeography of some macroscopic taxa is briefly discussed. Guidance is provided on procedures, equipment, and tools for collection and preservation of freshwater red algae. Information on the taxonomic scope and organization of this book is presented.

**Keywords** Collection · Guidelines · History · Preservation · Taxonomy

### Brief History of Freshwater Red Algal Studies

The history of freshwater red algae studies will be divided in three parts: (1) early treatises of cryptogams and pioneering studies; (2) research on freshwater red algal diversity in several parts of the world; (3) studies applying new types of evidence for alpha taxonomy.

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## *Early Treatises and Pioneering Studies*

The first records of freshwater red algae were published in the foundational work of Linnaeus (1753) who recognized the genus *Conferva* (a collection of different algal groups having filamentous thalli). Only three other genera in the *Conferva* contained organisms now regarded as algae, including the red algae. Roth (1797) described the genus *Batrachospermum* based on *Conferva gelatinosa* that was later transferred to *Batrachospermum gelatinosum*, the type species of the genus, the family Batrachospermaceae and the order Batrachospermales.

Lamouroux (1813) separated the algae currently known as red algae (Rhodophyceae) from other groups with similar gross morphology. He created the category “Floridées” to encompass the larger red algal group, presently known as class Florideophyceae. Although he recognized reproductive features specific to red algae (e.g., cystocarps) that are important for taxonomy, some morphologically simpler red algae (including the family called Batrachospermeae) were still classified among the filamentous algae in the Confervoideae, with other groups such as blue-greens (cyanobacteria), greens, and even lichens. The next relevant change in algal taxonomy was the work of Harvey (1836), who divided all algal genera into four major divisions: Chlorospermeae (green algae), Diatomaceae (diatoms), Melanospermeae (brown algae), and Rhodospermeae (red algae). Overall, his assignment of the genera known at the time was mostly in accord with modern classification systems, but the color variation present in many genera of red algae was problematic for his classification. Thus, genera such as *Porphyra* and *Bangia* as well as most freshwater red algae were placed in the Chlorospermeae (green algae) rather than in Rhodospermeae (red algae), due to thalli frequent greenish-blue or greenish in color.

Kützing (1843) proposed an alternative system by dividing the algae into two classes (Isocarpeae and Heterocarpeae), the latter including all red algae that were red in color. Class Heterocarpeae was further split into the tribes, Gymnospermeae and Angiospermeae, with red algae in the Angiospermeae. In contrast, the freshwater red algae were classified into the class Isocarpeae of the tribe Gymnospermeae, order Cryptospermeae, apart from most other red algae. Order Cryptospermeae had five families with two, Lemanieae and Batrachospermeae, including exclusively freshwater members. Rabenhorst (1868) was the first author to transfer the family Batrachospermaceae to Rhodophyceae. He divided the algae into four classes and was the first to use the ending “phyceae” currently applied to algal classes: Phycocromophyceae (blue-green algae—cyanobacteria), Chlorophyllophyceae (green algae), Melanophyceae (brown algae), and Rhodophyceae (red algae). Class Rhodophyceae included five families with freshwater representatives: Porphyraceae (genera *Porphyridium*, *Porphyra*, and *Bangia*), Chantransiaceae (“Chantransia,” *Batrachospermum*, and *Thorea*), Hildenbrandiaceae (*Hildenbrandia*), and Lemaneaceae (*Lemanea* and *Compsopogon*).

Several nineteenth century French botanists or naturalists made significant contributions to the knowledge of freshwater red algae, most notably JBG M Bory de



St. Vincent and Simon Sirodot. Bory (1808a, b, c) described several species in the genera *Batrachospermum* and *Lemanea* as well as proposing the genus *Thorea* and species therein. Sirodot (1884) “Les Batrachospermes” seminal monograph of the genus *Batrachospermum* established the basis of the taxonomy of the genus, which is still in use today. The illustrations in Sirodot’s book (hand-colored, fine line drawings) are “works of art” and among the most beautiful illustrations in the old botanical works. He based his taxonomic scheme for the genus on several characters: thallus color, trichogyne shape, location of carposporophytes, as well as other unique features, such as the morphology of the alternate life history phase (“Chantransia”). He divided the genus into six sections, using French names: Moniliformes, Helminthoides, Setaces, Turficoles, Verts, and Hybrides. He previously proposed the classification system for the genus (Sirodot 1873) and gave Latin names for the sections: *Moniliformia*, *Helminthoidea*, *Setacea*, *Turfosa*, *Virescentia*, and *Hybrida*. In another previous contribution (Sirodot 1875), he described the developmental characters of the genus *Batrachospermum*. Likewise, he studied in detail the morphology, development of *Lemanea* (as *Sacheria*) and *Paralemanea* (as *Lemanea*) proposing diagnostic characters for the genera and several species (Sirodot 1872).

### ***Research on Freshwater Red Algae in Several Parts of the World***

We listed the main contribution towards the taxonomic knowledge by the most relevant researchers who studied freshwater red algae for some regions of the world.

Following the studies of the nineteenth century by French naturalists, the taxonomy of freshwater red algae received the attention of several researchers in the early 1900s. Among these researchers was Heinrichs Skuja who may be considered one of the pioneers in the description of the red algal flora in numerous parts of the world. His first publication on the taxonomy of freshwater red algae (Skuja 1926) was the description of a new genus *Kyliniella* from Europe. This paper was followed by the several relevant publications on taxonomically and geographically diverse taxa (Skuja 1931, 1933, 1934, 1938, 1944, 1964, 1969). These publications provided detailed descriptions of previously known taxa such as *Sterrocladia*, *Tuomeya*, described a new genus, *Nothocladus* and proposed several species in *Batrachospermum* sensu lato (s.l.) and *Sirodotia*. At the time of his death, he had visited or received materials from herbaria worldwide and had made notes on new and unusual species that unfortunately went unnamed (Entwisle 1993).

In Europe, there were researchers who focused their studies on freshwater red algae in their countries. Manoel Póvoa dos Reis, a catholic priest, who supplemented his religious life with phycological research as an invited Assistant Professor at the University of Coimbra and who made an extraordinary contribution to the taxonomy of freshwater red algae from Portugal. He primarily focused on the genus *Batrachospermum* s.l., describing numerous new species, of which many are

known from other regions of Europe. His species descriptions were highly accurate and detailed. It is noteworthy that he was the first author to use photomicrographs to illustrate the morphological characters of the freshwater red algae. Among his most relevant publications are Reis (1958, 1960, 1965a, b, 1967, 1972, 1973, 1974). Gunnar Israelson conducted in depth research on freshwater red algae in Sweden (Israelson 1942). This publication provided descriptions and distributions of taxa currently classified into the Acrochaetales, Batrachospermales, and Hildenbrandiales with description of *Lemanea condensata* and *Kumanoa globospora* (as *Batrachospermum globosporum*). Karol Starmach contributed to the knowledge of red algae from Poland, from 1920s to late 1970s. He developed studies on freshwater red algae in general (Starmach 1928) and most particularly on the genus *Hildenbrandia* (Starmach 1952, 1969). His book on freshwater red algae (Starmach 1977) was a synthesis to the knowledge of freshwater red algae from Europe and some other parts of the world and of great importance to the advancement in the studies worldwide.

Important contributions towards the taxonomy of freshwater red algae from Asia were made by Japanese phycologists, Michiyasu Mori, Ryozo Seto and Shigeru Kumano. The first major study on this group was by Mori (1975) who described species of *Batrachospermum* from Japan and theorized about their phylogenetic relationships. Ryozo Seto published on several other genera of red algae, such as: *Hildenbrandia* (Seto et al. 1974; Seto 1977), *Thorea* (Seto 1979; Ratnasabapathy and Seto 1981; Seto et al. 1993), *Caloglossa* (Seto 1985; Seto and Jao 1984) and *Compsopogon* (Seto 1982, 1987; Seto et al. 1991; Seto and Kumano 1993). The most prominent Japanese freshwater red algal researcher was Shigeru Kumano, who not only was an expert on the Asian region but also the taxonomy of this group worldwide. He published numerous papers on freshwater red algae in general but extensively focused on the genus *Batrachospermum* s.l. either as sole author (Kumano 1978, 1982a, b, c, 1983, 1984a, b, 1990) or with collaborators from various countries (Kumano et al. 1970; Ratnasabapathy and Kumano 1982a, b; Kumano and Ratnasabapathy 1982, 1984; Kumano and Johnstone 1983; Kumano and Watanabe 1983; Kumano and Ohsaki 1983; Necchi and Kumano 1984; Kumano and Necchi 1985; Kumano and Bowden-Kerby 1986; Kumano and Liao 1987; Kumano and Phang 1987, 1990). He described many species of *Batrachospermum* section *Contorta*, and when it was raised to genus level his colleagues honored him with the genus *Kumanoa* (Entwisle et al. 2009). His monograph of freshwater red algae of the world (Kumano 2002) is still the most comprehensive publication for the taxonomy of the group and an inspiration for this current book.

The region of Australasia was the focus of the studies by Timothy Entwisle from the 1980s to the present. Entwisle and Kraft (1984) was his first contribution towards the knowledge of freshwater red algae from Australia. He published extensively on *Batrachospermum* s.l. from Australia and New Zealand (Entwisle 1992, 1993, 1995, 1998; Entwisle and Necchi 1992; Entwisle and Foard 1997, 1998, 1999a, b, 2007; Entwisle et al. 2004) as he recognized that the Australasian flora was unique from previously described parts of the world, especially Europe. He described a new genus of the Batrachospermales (*Psilosiphon*) (Entwisle 1989; Entwisle and Foard 1997; Entwisle et al. 2000) and a new species of the genus *Thorea* (Entwisle and

Foard 1999c). He has continued productive collaborations with other phycologists conducting research with a wider taxonomic and geographic scope (Sheath et al. 1996; Vis and Entwisle 2000; Entwisle et al. 2009, 2016; Necchi et al. 2016).

In South America, the freshwater red algal flora from Brazil has been investigated by Necchi and collaborators since the 1980s. The most representative contributions using classical taxonomic tools were: Kumano and Necchi (1985, *Batrachospermum*), Necchi (1987, *Batrachospermum*; 1990, *Batrachospermum*; 1991, *Sirodotia*), Necchi and Dip (1992, Compsopogonaceae), Necchi and Zucchi (1995a, *Audouinella*; 1995b, *Paralemanea*; 1995c, *Balliopsis*; 1997, *Thorea*). More recent studies using DNA sequence data and morphology resulted in relevant papers: Saunders and Necchi (2002, *Balliopsis*); Necchi et al. (2007, *Sirodotia*; 2010a, *Kumanoa*; 2010b, *Thorea*), Agostinho and Necchi (2014); Rossignolo and Necchi (2016).

Studies on the North American freshwater red algae were developed by Robert Sheath, who worked in several universities in Canada and the USA. Since his first publication on freshwater red algae (Sheath and Hymes 1980) from a region of Canada, he authored or co-authored many publications that overall represent one of the most relevant contributions to the taxonomy of freshwater red algae worldwide. His series of papers on the distribution and systematics of red algae in North America were novel in applying morphometrics from numerous populations to circumscribe species and compare with type specimens. This alpha taxonomic work included all groups represented in North America, resulting in numerous publications including the following: Sheath et al. (1992, section *Contorta*; 1993a, Thoreaceae; 1993b, Ceramiales; 1994a, section *Virescentia*; 1994b, section *Aristata*; 1994c, section *Turfosa*); Necchi et al. (1993a, b, *Audouinella*; 1993c, *Sirodotia*), Vis and Sheath (1992, Lemaneaceae; 1996, section *Batrachospermum*), Vis et al. (1992, Compsopogonaceae; 1995, section *Batrachospermum*). Other highly relevant aspect of this investigation involved broad revisions of major groups, such as: description of the new genus *Rhododraparnaldia* (Sheath et al. 1994) and revision of the morphology, ultrastructure, and classification of the Lemaneaceae (Sheath et al. 1996). The book chapter by Sheath and Vis (2015) represents a synthesis on the freshwater red algae in North America. A new genus *Sheathia* was named after him in recognition to his contributions to the systematics of the freshwater red algae (Salomaki et al. 2014).

In the last 20 years, other researchers made important contributions to the systematics of the freshwater red algae in other regions of the world whose publications were mostly compiled in books. Chinese research groups led by Zhixin Shi and Shu-Lian Xie summarized their findings on freshwater red algae from China in a volume of the Cryptogamic Flora of China (Flora Algarum Sinicarum Aquae Dulcis, volume 13, Shi et al. 2006) and a checklist on the order Batrachospermales (Xie et al. 2020). Eloranta and collaborators studied intensively the freshwater red algae from Finland and other countries of Central Europe (Eloranta and Kwadrans 2007; Eloranta et al. 2011, 2016; Eloranta 2019).

## *Studies Applying New Types of Evidence to Systematics*

As new techniques have been developed to study the systematics of algae in general and marine red algae in particular, these methods have been applied to the various lineages of freshwater red algae. In many cases, these new data have challenged the previous ideas about the evolutionary relationships of these algae and led to the proposal of new taxonomic schemes. Our understanding of the phylogeny of freshwater red algae has greatly benefited from these new types of evidence.

An ultrastructural study of the pit plugs by Pueschel and Cole (1982) resulted in considerable changes in the systematics of the red algae in general. These researchers observed patterns in the structure of pit plugs with variation in number of layers (0–2) and presence/absence of cap membranes. These pit plug characters were supported by features of morphology and reproduction such that the taxonomic scheme at the level of order was revised. Among the several changes resulting from this major finding was the proposal of the new order Batrachospermales to accommodate the strictly freshwater families Batrachospermaceae, Lemnaceae, and Thoreaceae.

Studies involving a combination of morphology (including ultrastructure) and DNA sequence data most significantly contributed to reach a natural classification system, better delimitation of specific and generic taxa and relationships among the genera and species within the genera. The first attempt to understand the phylogeny of the main group of freshwater red algae (the order Batrachospermales) was conducted by Vis et al. (1998). They analyzed DNA sequences of the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbcL*) gene and small subunit of the ribosomal DNA (SSU rDNA) to infer the phylogeny of the group. An important finding was that a member of the Thoreaceae (*Thorea violacea*) was not closely related to the other taxa of the Batrachospermales, and it did not appear to be a natural grouping within the Batrachospermales. In addition, they established that the genus *Batrachospermum* is paraphyletic but recommended it be retained pending further investigations and raised the possibility that the sectional classification may represent clades which could be the foundation for the description of new genera in the Batrachospermales.

Two noteworthy contributions derived from this combined morphology and molecular data approach were the proposals of the orders Balbianiales (Sheath and Müller 1999) and Thoreales (Müller et al. 2002). The order Balbianiales (Chap. 4) was proposed to accommodate two genera (*Balbiana* and *Rhododraparnaldia*) that were grouped together on a well-supported branch separate from other taxa of the closely related orders Acrochaetales, Batrachospermales, Nemaliales, and Palmariales. The most distinguishing feature of members of this order is the production of spermatangia on the tips of specialized, elongate cells. The findings of Müller et al. (2002) indicated that the Thoreaceae have been misclassified into the Batrachospermales and they proposed the order Thoreales (Chap. 4). It is characterized by having exclusively freshwater representatives with multiaxial gametophytes and pit plugs having two cap layers with a plate-like outer layer.

A major effort of freshwater red algal experts resulted in a comprehensive phylogenetic analysis of the order Batrachospermales incorporating members of as many genera and sections of *Batrachospermum* as possible (Entwisle et al. 2009). This synthetic study was aimed at producing better defined taxonomic categories and particularly to reduce paraphyly within the genus *Batrachospermum*. A new genus was proposed (*Kumanoa*) from combining the sections *Contorta* and *Hybrida* and raising to the genus level, as well as raising a subsection to section in *Batrachospermum* (section *Macrospora*). They amended the circumscription of the family Batrachospermaceae to include all batrachospermalean taxa subsuming the genera previously known in the Lemnaceae. Eight sections were recognized in *Batrachospermum* (*Acarosporophytum*, *Aristata*, *Batrachospermum*, *Helminthoidea*, *Macrospora*, *Setacea*, *Turfosa*, and *Virescentia*) and an informal paraphyletic grouping of taxa within *Batrachospermum* containing species primarily known from Australasia (“Australasica group”).

After this review by Entwisle et al. (2009), subsequent research followed the earlier suggestion (Vis et al. 1998) to reexamine *Batrachospermum* section that formed well-supported clades in phylogenetic analyses. Thus, the effort to rectify the paraphyly of *Batrachospermum* led to the proposal of several new genera resulting from the raising of sections to the generic level. In chronological order, the changes proposed were: *Sheathia*, former section *Helminthoidea* (Salomaki et al. 2014); *Torularia*, former section *Setacea* (Rossignolo and Necchi 2016; Wynne 2019); *Virescentia*, former section *Virescentia* (Necchi et al. 2018); *Acarosporophycos*, former section *Acarosporophytum*, and *Visia*, former section *Aristata* (Necchi et al. 2019a); *Montagnia*, former section *Macrospora* (Necchi et al. 2019b); and *Paludicola*, former section *Turfosa* (Vis et al. 2020). In addition, Entwisle et al. (2016) proposed *Nocturama* to accommodate *Batrachospermum antipodites* and an expanded circumscription of the genus *Nothocladus* to include all other members of the “Australasica group”).

Phylogenomic studies of freshwater red algae are still relatively scarce but few mitochondrial and plastid genomes have been published recently. Muñoz-Gómez et al. (2017) included *Boldia* and *Compsopogon* in a study of chloroplast genome size in the Proteorhodophytina. Likewise, Lee et al. (2016) published the chloroplast genome of *Thorea hispida* as part of a more general study on the plastid genome architecture of red seaweeds and seed plants and Nan et al. (2017) compared the organelle genomes of a member of the Compsopogonales, Thoreaales, and Batrachospermales to analyze their architecture and gene content features. Within the Batrachospermales, Paiano et al. (2018a) sequenced plastid genomes of seven taxa describing and comparing their characteristics with other red algal groups, as well as using them to infer the phylogenetic relationships to better resolve the infra-ordinal classification within this order. In addition, Paiano et al. (2018b) described six mitochondrial genomes for members of the Batrachospermales and compared them with other red algal groups. The chloroplast and mitochondrial genomes were sequenced for a recently described monospecific genus *Lympha mucosa* (Wolf et al. 2017; Evans and Vis 2020); therefore, the number of organellar genomes available in the Batrachospermales continues to rise but still only represents a small fraction of

the generic and species diversity of the order. For the Balbianiales, Evans et al. (2019) have provided the organellar genomes of *Balbiana investiens*. Among the strictly freshwater orders, the results to date are promising, but still scarce with plastid and mitochondrial genomes of only 12 of the >170 species sequenced so far. Thus, a more representative taxon sampling is needed to produce a more robust phylogeny and to elucidate their relationships with other groups of red algae.

## Taxonomic Diversity and Phylogeny

In this book, we survey all non-marine rhodophytes and include those from strictly freshwater habits such as lakes and rivers as well as hot springs. In addition, those taxa collected from terrestrial habits such as soils and wet walls as well as epiphyte and epizoic are included. These algae represent approximately 3–5% of the estimated >7000 species within the Rhodophyta lineage.

The Rhodophyta is classified into three subphyla (Table 1.1). The Cyanidiophytina is comprised of only freshwater taxa whereas the Proteorhodophytina and Eurhodophytina have both marine and freshwater members. Although some members of Cyanidiophytina are mesophiles, the majority are thermoacidophiles from hot spring regions in various parts of the world. There are only a few genera (we recognize four in this book) and a handful of species that have been divided at times into various strains or morphs (Chap. 2). This subphylum has been the subject of recent taxonomic revisions and probably more to come (Liu et al. 2020).

The Proteorhodophytina contains four classes, each with freshwater members (Table 1.1). Of the nine orders, five are represented in freshwaters (Chap. 2). Most of these taxa have simple morphologies ranging from unicells, pseudofilaments to filaments. Ten genera are recognized but only a few have representative DNA sequence data. Therefore, the classification is primarily based on morphology and information about phylogenetic relationships among these genera is limited. However, a study of the chloroplast genomes within the subphylum has provided the largest known chloroplast genomes and revealed a great range in chloroplast size among members sequenced (Muñoz-Gómez et al. 2017). Findings such as these will most likely spark more studies that will also help clarify the systematics within the subphylum and among genera.

The Eurhodophytina is divided into two classes (Table 1.1). The class Bangiophyceae has primarily marine members and only two genera are known from freshwaters (Chap. 3). The nominate genus, *Bangia* is currently recognized as monospecific and geographically widespread. The other genus, *Granuflum* has been placed in this class, but there is no DNA sequence data to link it to other members of the class and at least some of the morphological traits suggest that it may be reclassified with future study (Chap. 3). The Florideophyceae houses the majority

**Table 1.1** Taxonomic scheme of freshwater red algal taxa included in this book

Subphylum	Class	Subclass	Order	Family	Genera		
Cyanidiophytina	Cyanidiophyceae		Cyanidiales	Cyanidiaceae	<i>Cyanidium</i> (1)		
			Cyanidioschyzonales	Galdieriaceae	<i>Galdieria</i> (1)		
	Composopogonophyceae		Composopogonales	Cyanidioschyzonaceae	<i>Cyanidiococcus</i> (1) <i>Cyanidioschyzon</i> (1)		
				Boldiaceae	<i>Boldia</i> (1)		
Proteorhodophytina	Composopogonophyceae			Composopogonaceae	<i>Composopogon</i> (1) <i>Pulvinaster</i> (1)		
			Porphyridiophyceae		Porphyridiales	Porphyridiaceae	<i>Flintilla</i> (1) <i>Porphyridium</i> (3)
					Rhodellophyceae	Glaucosphaerales	Glaucosphaeraceae
	Stylonematophyceae		Stylonematales	Stylonemataceae	<i>Chroodactylon</i> (1) <i>Chroothece</i> (4) <i>Kylinella</i> (1) <i>Rhodospira</i> (1)		
				Rufusiales	Rufusiaceae	<i>Rufusia</i> (1)	
	Bangiophyceae		Bangiiales	Bangiaceae	<i>Bangia</i> (1)		
				Granuflaceae	<i>Granuflum</i> (1)		
				Corallinales	Corallinaceae	<i>Paeophyllum</i> (1)	
		Floriideophyceae	Corallinophycidae	Hildenbrandiales	Hildenbrandiaceae	<i>Hildenbrandia</i> (3)	
				Rhodymeniophycidae	Delesseriaceae	<i>Cataglossa</i> (6)	
Nemaliophycidae			Gigartinales	Rhodomelaceae	<i>Bostrychia</i> (7) <i>Polysiphonia</i> (1)		
			Acrochaetiales	Caulacanthaceae	<i>Sterrocladia</i> (2)		
Eurhodophytina			Balbaniiales	Acrochaetiaceae	<i>Audouinella</i> (5)		
				Ottiales	<i>Ottia</i> (1)		
				Balbaniaceae	<i>Balbania</i> (1)		
		Thoreales		Thoreales	Thoreaceae	<i>Rhododraparnaldia</i> (1)	
				Batrachospermales	Batrachospermaceae	<i>Thorea</i> (12) <i>Nemalionopsis</i> (2)	

(continued)

**Table 1.1** (continued)

Subphylum	Class	Subclass	Order	Family	Genera
					<i>Acarosporophycos</i> (1) <i>Batrachospermum</i> (6) <i>Genadendalia</i> (1) <i>Kumanoa</i> (41)
					<i>Lemanea</i> (8) <i>Lympha</i> (1) <i>Montagnia</i> (2) <i>Nocturama</i> (3) <i>Nothocladus</i> (18)
					<i>Notohesperus</i> (1) <i>Paludicola</i> (15) <i>Paralemnea</i> (9) <i>Petrohia</i> (1) <i>Psilosiphon</i> (1)
					<i>Sheathia</i> (19) <i>Sirodotia</i> (9) <i>Torulatia</i> (5) <i>Tuomeya</i> (1)
					<i>Virescentia</i> (8) <i>Visia</i> (4)
					<i>Volatus</i> (3)

Infrageneric taxa including species and varieties in parenthesis



of the species diversity for the Rhodophyta. As with the marine red algae, this is also true for those from freshwaters (Table 1.1). Although there are freshwater taxa in all four subclasses, they are concentrated in eight of the 31 orders. Most of those orders have just a few genera and species that inhabit freshwaters among the many marine taxa. The exceptions are the three exclusively freshwater orders of the Balbianiales, Batrachospermales, and Thoreaales (Chaps. 4 and 5) with the Batrachospermales containing two thirds of the overall freshwater species diversity. In the most recent phylogeny of the Nemaliophycidae, the phylogenetic relationships among these freshwater orders and other primarily marine orders were not resolved but suggest multiple invasions and diversification in freshwater (Lam et al. 2016). Undoubtedly, future research will pursue a better understanding of the transition to freshwater, which may also elucidate the systematic relationships among these orders.

## Biogeography

An exhaustive discussion of the biogeography of freshwater red algae is beyond the scope of this book. In this section, we provide some insights from compiling the data for the other chapters and update a case study of the Batrachospermales (Vis 2016) highlighting potential future research. Biogeography is the study of organisms in geographic space and through geologic time, but here we will primarily focus on geographic patterns observed among individual taxa and insights that are now possible with the amount of DNA sequence data available. The data for the microscopic freshwater red algae are not yet sufficient to postulate geographic trends such that macroscopic taxa will be emphasized.

Among the freshwater red algae are species that belong to either primarily marine genera or populations of marine species that have invaded freshwater including *Bostrychia*, *Caloglossa*, *Hildenbrandia*, *Pneophyllum*, and *Polysiphonia* (Chap. 3). *Bostrychia* and *Caloglossa* are known to be euryhaline, typically inhabiting mangroves and other environments that receive regular influxes of freshwater and *Polysiphonia* is found in the intertidal. For these three genera, DNA sequence data from strictly freshwater habitats show that these populations to be conspecific with populations in brackish/marine habitats. Interestingly, it appears that once these taxa invade freshwaters they tend to reproduce asexually or recycle the tetrasporophyte as sexual reproductive structures have been very rarely reported. Likewise, freshwater species of *Hildenbrandia* are noted to reproduce via asexual gemmae. For *Bostrychia*, *Caloglossa*, *Hildenbrandia*, and *Polysiphonia* species or populations have been reported from numerous continents. It is unknown if there have been multiple invasions of freshwater by a taxon or if a single invasion with subsequent spread to other freshwater habitats. In the case of *Polysiphonia subtilissima*, there are four freshwater reports and at least two are quite near to marine source populations so multiple invasions is more likely. For *Hildenbrandia*,

freshwater species are grouped in a clade separate from the marine ones. Thus, it is probable that they have spread after invasion of freshwater based on their widespread distribution and frequent reports, but that would need to be substantiated with more representative DNA sequence data.

A surprising discovery of a coralline red alga, *Pneophyllum*, in freshwaters was reported a few years ago (Žuljević et al. 2016). Unlike the other marine invaders highlighted above, the freshwater populations have gametangia. As discussed by the original authors, the unique geology and geographic placement of the drainage basin with karst limestone adjacent to the marine environment facilitated invasion and speciation. It is unlikely that this coralline or others would be encountered in other freshwater locations.

There are interesting geographic patterns among freshwater red algae especially in comparing distributions for closely related taxa. *Boldia* and *Compsopogon* are monospecific (Chap. 2), have similar gross morphologies, and reproduce via putative asexual spores that are shed from the thallus. However, *Compsopogon* is widely distributed on numerous continents, whereas *Boldia* is geographically restricted to eastern North America. This disparity is probably not explained by the ability to disperse since both produce similar spores, but more likely due to habitat restrictions, although research is needed to confirm this conclusion. Similarly, the genera *Thorea* (Chap. 4), *Batrachospermum*, *Sirodotia*, and *Torularia* (Chap. 5), all contain one or two species based on DNA sequence data that have a broad geographic distribution on multiple continents, but all other species have restricted geographic ranges to a single continent or even a few locations. These patterns are a bit puzzling; why would one species of a genus be able to either disperse better or be able to tolerate wider environmental conditions than the others? Hopefully, more data on dispersal mechanisms and environmental conditions will provide insights in the future.

Of the freshwater red algae, the Batrachospermales has much of the genus and species diversity as well as being well studied. Vis (2016) presented this order as a case study in biogeography; here that case study is updated based on the latest taxonomic scheme provided in this book at the genus level (Table 1.2). The number of genera per continent is evenly distributed with four continents having 10–11 genera with Australasia having slightly less (9) and North America slightly more (13). A third of the genera are monospecific occurring in a single continent, yet they are distributed on four of the continents. The other two thirds of the genera show none to be restricted to a single continent and three (*Kumanoa*, *Sirodotia*, and *Torularia*) are present on all continents. This pattern of distribution may suggest that the Batrachospermales is an evolutionary old lineage, but molecular clock data, which is difficult without closely related fossils, would be needed to confirm (Vis 2016).

A comparison among the continental floras using Sorenson's similarity index provides some insights (Table 1.3). The primarily Northern Hemisphere continents of North America, Europe, and Asia are highly similar. Australasia, the most isolated continent, shows the least similarity with the other continents. Africa shows the highest similarity with Australasia perhaps suggesting a Gondwanan connection, but South America has more similarity with Asia. Nevertheless, it is likely that part of

**Table 1.2** Continental distributions for genera in the Batrachospermales

Genus	Africa	Asia	Australasia	Europe	North America	South America
Monospecific						
<i>Acarposporophycos</i>						X
<i>Genadendalia</i>	X					
<i>Lympha</i>					X	
<i>Notohesperus</i>			X			
<i>Petrohua</i>						X
<i>Psilosiphon</i>			X			
<i>Tuomeya</i>					X	
Species (2–41)						
<i>Volatus</i>				X	X	
<i>Nothocladus</i>	X		X			
<i>Nocturama</i>	X		X			X
<i>Montagnia</i>	X	X			X	X
<i>Visia</i>	X	X	X			X
<i>Batrachospermum</i>		X		X	X	
<i>Lemanea</i>		X		X	X	
<i>Virescentia</i>		X		X	X	X
<i>Paludicola</i>		X		X	X	X
<i>Paralemanea</i>	X	X		X	X	X
<i>Sheathia</i>	X	X	X	X	X	
<i>Kumanoa</i>	X	X	X	X	X	X
<i>Sirodotia</i>	X	X	X	X	X	X
<i>Torularia</i>	X	X	X	X	X	X
Total	10	11	9	10	13	11

**Table 1.3** Sorenson's similarity index of continental floras for genera in the Batrachospermales

Continent	Australia	Africa	South America	North America	Europe	Asia
Australia	—					
Africa	0.74	—				
South America	0.50	0.67	—			
North America	0.36	0.64	0.58	—		
Europe	0.40	0.50	0.57	0.87	—	
Asia	0.50	0.67	0.73	0.83	0.86	—

the flora (*Nocturama*) may be derived from that connection with species represented in Australasia, Africa, and South America (Chap. 5, Necchi et al. 2016). More patterns may emerge from analyzing species level data and examining potential dispersal mechanisms such as bird flyways. Overall, research on the biogeography of freshwater red algae is in a nascent stage, but the newly generated DNA sequence data from taxonomic and floristic studies will bring our understanding of this topic into focus.

## Collection of Freshwater Red Algae

There have been several publications that provide detailed information on procedures and equipment for collection and preservation of freshwater red algae (e.g., Entwisle et al. 1997; Eloranta and Kwandrans 2012; Sheath and Vis 2015; Necchi 2016). Here, we will briefly summarize the protocols and recommendations provided in those previous publications aiming to describe the most relevant aspects for a non-experienced collector. Given that most red algal representatives are macroalgae and are typically found in streams or rivers, we will concentrate on macroscopic forms and lotic habitats, but see end of this chapter regarding less typical habitats and potential algae to find.

As freshwater red algae are usually not very frequent and abundant in drainage basins it is advisable to plan a collection trip to optimize effort and costs. Although freshwater red algae can be distributed in different parts of a major drainage basin, they tend to be more common in the smaller channels of first to fourth order reaches; these would be wadable streams or at the edges of wider, deeper streams. When considering the collection in a particular stream or river, it is often necessary to thoroughly search a stream reach. Usually, stream segments of 20–50 m length should be examined, using a view-box with glass bottom and plastic sides, for a representative sampling. It is recommendable to choose a stream or river segment with more heterogeneous conditions, such as types of substrate (e.g., rock, boulders, cobble, woody debris), shading (open and closed canopy), and flow pattern (e.g., pools, riffles, and runs) to increase the chances of finding appropriate microhabitats for a wide variety of taxa and growth forms (Fig. 1.1a–c). For example, in a large, fast-flowing stream, *Audouinella*, *Lemanea*, and *Paralemanea* may be found attached to the upper surface of rocks and boulders of the rapidly flowing portions in the mid channel, while *Batrachospermum*, *Kumanoa*, *Sheathia*, *Sirodotia*, and *Tuomeya* may be on the sides of rocks or localized in quiet side channels and pools, attached to a variety of substrata, such as logs and tree roots (Sheath and Vis 2015).

There are a number of tools to bring to a site in order to collect the algae, catalog conditions and document the site (Fig. 1.1d). For collecting, tools such as long forceps, razor blades, spatulas, and vacuum pipettes are useful for successfully removing the specimens from the variety of substrates (bedrock, boulders, cobble, logs, tree roots, macrophytes, and other macroalgae). Bringing sample containers of different sizes and volumes are useful if the algae are of different sizes; different researchers prefer particular types of containers, but small plastic bags or the equivalent of 50 mL centrifuge tubes are good and when visiting more than one site in a day, a larger plastic bag that all the samples from a site can be placed together is great to keep things organized. If possible, place each specimen that you think might be a different species, into its own container; if that is not feasible, then be sure to write in your collecting book the suspected number of species and a short description of each so that you can identify it back in the lab. For example, you might write, two *Batrachospermum*-like species: one dark-green, small, one reddish-brown very large. In the end, they might be the same species, but it is better to note them



**Fig. 1.1** (a) A ~20 m wide stream with moderate flow, tree canopy along the sides but open in the middle and substrate consisting of boulders, rocks, and cobble; at this location, taxa such as *Paralemanea*, *Audouinella*, *Batrachospermum*, and *Tuomeya* would be likely to occur. (b) A woodland stream with very fast flow over bedrock supports growths of *Paralemanea* (arrow), which often has a blackish color. (c) A small spring emerging from a man-made structure with year-round flow and constant temperature as well as small cobbles is where *Virescentia viride-americana* (arrow) has been collected over multiple years. (d) Equipment for collecting freshwater red algae include a view-box, large forceps, meters, plastic tube, and bag. (e) *Batrachospermum*-like genera (*Tuomeya*—upper left, *Batrachospermum gelatinosum*—upper right and *Lymphe*—lower) can be collected in the same location, but different taxa can be separated by color and thickness until identification



separately until further identification (Fig. 1.1e). Other equipment to bring on a collecting trip includes hip waders, diver's gloves for winter collecting, camera or cell phone to document the location and a GPS to give the precise location (altitude, longitude, and elevation) of the sampling site. Although a cell phone might provide all the needed information, please note that many locations will probably be outside of cell phone service. Equipment for measuring selected stream environmental variables usually include portable single meters or multiple probes: thermometer, pH meter, conductivity meter, turbidity meter, and flowmeter as well as tape measure for width and depth. Be sure to write down all your observations in your notebook, including the date, types of substrates, canopy cover (open, percent shade), water-color (colorless, tea-colored), water clarity (clear or turbid), stream depth, stream width (may have to be estimated for larger streams), and measurements from meters. For the algae collected, be sure to write down how many species and a short description of each, especially color, and note the abundance of each. If it is a warm day, you may want to store your samples in an ice cooler until you return from the field.

Specimens are best observed shortly after collection in a living state before preservation if you intend to do so. A brief examination during collection with a portable field microscope or a dissecting microscope are useful in some cases, e.g., more than one taxon present, preliminary identification, or interest in a particular species. If the specimens cannot be examined in the field, be sure to make microscopic observations prior to fixation. For morphological purposes, they should be fixed in 2.5% buffered glutaraldehyde, and kept in a dark and cool environment. Other fixatives include 4% buffered formaldehyde, FAA, or Lugol's solution, but these might cause more distortions in morphology and pigmentation. For molecular purposes, specimens can be cleaned of debris and epiphytes, if necessary, viewing in a dissecting microscope, and then dried in silica gel desiccant or frozen. Absolute ethanol can be alternatively used for taxa with very small thalli, e.g., small tufts of *Audouinella* or "Chantransia" stage. For archival purposes, drying of herbarium specimens is desirable, but can result in considerable morphological damage, in some cases not allowing observation of critical features. It is recommended, if making pressed specimens, that there are also liquid preserved or silica gel-desiccated specimens. The correct preservation is essential for observation of the vegetative and reproductive diagnostic characters required for a proper identification.

Freshwater red algae, particularly members of the Batrachospermales and Thoreaales, can be seasonal with the macroscopic gametophytes only present at a particular time of the year. In tropical regions, they are most abundant during the dry season and the rainy season should be avoided as it will be difficult to observe them due to high flow, turbidity, and depth. In temperate areas, early spring has been the season when these algae are most abundant, and they may not be present in summer due to heavy canopy cover by surrounding vegetation or winter due to frequent

storms contributing to high flow, turbidity, and depth. However, seasonality can be tricky. For example, in temperate eastern North America, *Paralemanea* thalli often start growing in December and may disappear by June, likewise *Virescentia viride-america* is a spring ephemeral, abundant from March–June, in contrast *Tuomeya* and *Thorea* can reach maximum size in September–October. If you are collecting locally, you may wish to visit your streams seasonally to see what species are growing; don't be surprised if you find different freshwater red algae depending on the season.

Although the majority of the freshwater red algae are macroscopic and occur in streams and rivers, there is still much to explore in terms of algae size and habitats. Excluding those from very specific environments (sulfur fumaroles, sloth fur), microscopic and macroscopic red algae may be present in unexpected locations. There are several species that can be at the edges of lakes, ponds, and bogs and include *B. gelatinosum*, some species of *Kumanoa*, and many species of *Paludicola*. The conditions in the Great Lakes are favorable for *Bangia atropurpurea* to form a band at the water line above the *Cladophora* (green alga) that often has epiphytic *Chroodactylon ornatum*. Genera such as *Sheathia*, *Batrachospermum*, and *Virescentia* can be collected in springs, even those that are quite small but have flow year-round (Fig. 1.1c). *Kyliniella* is a rarely reported alga that may have specific conditions in which it forms macroscopic growths. So, when exploring any freshwater habitat, keep a sharp eye out for freshwater red algae.

### ***Scope of this Book***

In order to guide the reader, the following is an explanation of how the information was obtained and organized.

### ***Taxa Covered in the Book***

Taxa of red algae inhabiting inland habitats in the broadest sense were included, such as rivers, streams, waterfalls, lakes, ponds, springs, and less usual habitats, like hot springs, as well as forms growing in endolithic and aerophytic habitats. In coastal areas, only those habitats that are not directly influenced by salt water were considered and judged by the information provided in the respective publication. Thus, taxa and reports of taxa inhabiting brackish waters were not included. We adopted the term freshwater as described above instead of using non-marine.

## ***Taxonomic Focus and Information for the Genera and Species Described***

The overall taxonomic scheme is provided in Table 1.1. In each of the chapters, a short description of the higher taxonomic levels is provided. There are other resources that provide a fuller account of the higher level taxonomy, and the focus of this book is primarily genus and species descriptions and identification. Each genus is organized following the supra-generic levels according to the current systematic treatments with the family, order, subclass, and class.

For each genus, the following information is provided: (a) synonyms; (b) type species; (c) revised description; (d) diagnostic characters—emphasis on the vegetative and reproductive characters that distinguish it from closely related genera; (e) habitat—compiled from records for all species in the genus; (f) distribution; (g) phylogenetic relationships among species—phylogenetic tree (maximum likelihood and Bayesian inference) based on *rbcL* sequences; this molecular marker was chosen because it proved to be appropriate to infer phylogeny and has the largest number of sequences available in the GenBank database; (h) key to the species in the genus.

For each species, the following information is presented: (a) type: with updated data about collector, date, specimen number (barcode) checked in each herbarium where the type is housed; (b) type locality—given as precisely as possible with the information provided in the protologues or herbarium labels, sometimes estimated by the nearest general location using Google Earth; (c) revised description—based on the species concept adopted in the book, which means that some references, sometimes many previous records, were not included; illustrations (mostly photomicrographs) of the most important diagnostic characters for all species; we tried to use, as much as possible, our own material to illustrate each species but when not available, we gratefully borrowed images from colleagues or ultimately used published images with permission by the publishers or modified line drawings from published material; (d) diagnostic characters; (e) representative sequences in GenBank—COI-5P, that are proved to be appropriate to discriminate species, and *rbcL* to infer the phylogenetic relationship; when these markers were not available, others that have been used in the group were provided; (f) distribution—worldwide geographic distribution of the species, including a map, based on the revised concepts used in the book, sometimes requiring DNA sequences; when species records did not meet this criterion, they were not considered; (g) key references—prioritizing publications providing descriptions of vegetative and reproductive characters, as well as DNA sequence data.



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# Chapter 2

## Subphylum Cyanidiophytina, Class Cyanidiophyceae; Subphylum Proteorhodophytina, Classes Compsopogonophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae



Orlando Necchi Jr and Morgan L Vis

**Abstract** Subphylum Cyanidiophytina is composed of a single class (Cyanidiophyceae) and three genera have been traditionally recognized *Cyanidium* and *Galdieria* (Cyanidiales) and *Cyanidioschyzon* (Cyanidioschyzogonales); a new genus (*Cyanidiococcus*) has been recently described in the order Cyanidioschyzogonales. All species are exclusive to inland habitats, occurring mostly in thermal waters, as thermoacidophiles, and also as mesophiles (aerophytic or endolithic). Subphylum Proteorhodophytina is represented in freshwaters by all four classes (Compsopogonophyceae, Porphyrideophyceae, Rhodellophyceae, and Stylonematophyceae). Class Compsopogonophyceae has three freshwater members in the single order Compsopogonales: genera *Boldia* (family Boldiaceae), *Compsopogon* and *Pulvinaster* (family Compsopogonaceae); all are monospecific. Class Stylonematophyceae is represented by five genera, four in the order Stylonematales, *Chroodactylon* (one species), *Chroothece* (four species), *Kyliniella* and *Rhodospira* (one species), and one in the order Rufusiales, the monospecific genus *Rufusia*. Class Porphyridiophyceae has freshwater members in the genera *Flintiella* (one species) and *Porphyridium* (three species). Class Rhodellophyceae has the monospecific genus *Glaucosphaera*.

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**Keywords** Cyanidiophyceae · Compsopogonophyceae · Freshwater · Porphyrideophyceae · Rhodellophyceae · Rhodophyta · Stylonematophyceae · Taxonomy

## **Subphylum: Cyanidiophytina; HS Yoon, KM Müller, RG Sheath, FD Ott, and D Bhattacharya, J Phycol 42:489**

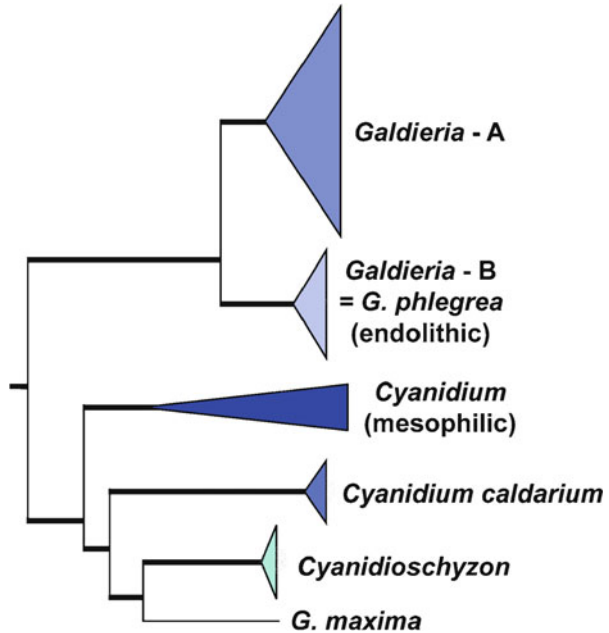
The characteristics of the subphylum are as follows (adapted from Nakayama and Yokoyama 2017): unicellular, coccoid; cells covered by a distinct wall or naked, with a single parietal blue-green chloroplast without a pyrenoid, with peripheral thylakoids; phycobilisomes with allophycocyanin, c-phycocyanin; with  $\beta$ -carotene and zeaxanthin; mitochondrion spherical or reticulate, with flat cristae. Asexual reproduction by binary fission or endospores; sexual reproduction unknown. Most species inhabit acidic and high temperature conditions in hot springs or acidic sulfur fumes; some are mesophilic (aerophytic or endolithic); some are facultative heterotrophs (e.g., *Galdieria*).

A multigene phylogeny showed the Cyanidiophyceae to represent the most ancient split within the Rhodophyta that was estimated to have occurred ca. 1.3 million years ago (Yoon et al. 2004). The class Cyanidiophyceae had been composed of a single order Cyanidiales, but Ott (2009) proposed a new order (Cyanidioschyzogonales) to accommodate the genus *Cyanidioschyzon*. Molecular data suggest potential undescribed lineages in the class (Ciniglia et al. 2004; Reeb and Bhattacharya 2010; Hsieh et al. 2015).

There are discrete morphological characteristics to distinguish the Cyanidiales genera, as well as ecophysiological, cytomorphological, and biochemical differences (Merola et al. 1981; Albertano et al. 2000; Reeb and Bhattacharya 2010; Liu et al. 2020). *Cyanidioschyzon* has ovoidal to clavate shape cells and reproduces by binary fission, whereas in *Cyanidium* and *Galdieria* cells are mostly spherical and differ in average cell size and number of endospores produced per sporangium (Reeb and Bhattacharya 2010). A fourth genus (*Cyanidiococcus*) was recently described based on genomic, morphological, and physiological traits (Liu et al. 2020). The four genera also differ in other cytomorphological characteristics: chloroplast and mitochondrion shape, presence/absence of vacuoles, and a rigid cell wall (Albertano et al. 2000; Reeb and Bhattacharya 2010; Liu et al. 2020).

Phylogenetic analyses support the division of the Cyanidiophyceae into four distinct lineages (Ciniglia et al. 2004; Yoon et al. 2004, 2006a; Reeb and Bhattacharya 2010; Fig. 2.1). The first is the *Galdieria* lineage (excluding *G. maxima*) that is divided into two clades: *Galdieria* A (*G. sulphuraria*, *G. daedala*, and *G. partita*) and *Galdieria* B (*G. phlegrea*). *Galdieria* A includes strains from worldwide locations and the order of branching within this clade follows a clear geographical pattern. *Galdieria* B contains taxa from dry and endolithic habitats exclusively from Italy. These two clades do not have distinguishing morphological features but differ with respect to ecophysiology

**Fig. 2.1** Phylogenetic tree of the main lineages of the class Cyanidiophyceae based on *rbcL* sequences showing the four major lineages (modified from Reeb and Bhattacharya 2010). The thick branches denote well-supported monophyletic groups



(growth and photosynthetic rates). The second major lineage is represented by two clades: one containing mesophilic *Cyanidium* spp. and another with three minor clades with extremophilic representatives (*C. caldarium*, *Cyanidioschyzon*, and *G. maxima*). Only one lineage (the mesophilic *Cyanidium* spp.) has a defined geographic distribution, inhabiting nonacidic and nonthermal caves in Italy. The other two clades do not show a pattern consistent with the geographical distribution.

Based on genomic, morphological, and physiological traits, a new genus and species (*Cyanidiococcus yangmingshanensis*) was proposed by Liu et al. (2020) and should be applied to several strains that were misidentified as *G. maxima*. The taxonomic scheme with two orders and three families was proven to be consistent with the new data: the Cyanidiales with Cyanidiaceae (*Cyanidium* Geitler) and Galdieriaceae (*Galdieria* Merola) and the Cyanidioschyzogonales with Cyanidioschyzonaceae (*Cyanidioschyzon* De Luca, Taddei and L. Varano and *Cyanidiococcus* S-L Liu, Y-R Chiang, HS Yoon and H-Y Fu).

#### Key to the genera of Cyanidiophyceae

1a	Reproduction by binary fission, cells clavate, or ovoidal with one elongate chloroplast at one side of the cell	<i>Cyanidioschyzon</i>
1b	Reproduction by endospores, cells mostly spherical with chloroplast occupying most of the cell	2
2a	Cells with vacuoles and a multi-lobed chloroplast	<i>Galdieria</i>
2b	Cells without vacuoles and spherical or variable in shape chloroplast	3
3a	Chloroplasts spherical, endospores produced in groups of 4	<i>Cyanidium</i>
3b	Chloroplasts polymorphic, endospores produced in groups of 2–4	<i>Cyanidiococcus</i>

**Order Cyanidiales** TA Christensen in Böcher and M Lange, Botanik, Bind II, Systematisk botanik, Number 2, Alger (1962) *emend* Ott, Handbook of the taxonomic names of non-marine Rhodophycophyta:588 (2009)

**Description:** cells without vacuoles and chloroplasts parietal, not lobed; reproduction by two to many endospores. Two families have been established in the order: Cyanidiaceae and Galdieriaceae. Family **Cyanidiaceae** Geitler has only one genus and species that are described below. The genus has been widely accepted to have a single species.

*Cyanidium caldarium* Geitler, Arch Hydrobiol Suppl 14:624 (1934) *emend* A Merola, R Castaldo, P De Luca, A Gambardella, A Musacchio and R Taddei, Giorn Bot Ital 115:191 (1981) (Fig. 2.2a, f)

**Type:** NAP, P De Luca (Neotype); corresponds to strain 182 of the Algal Collection University Federico II (ACUF), Naples, Italy.

**Type locality:** Indonesia, Central Java, Mount Lawu, 7.627500° S, 111.194167° E (estimated).

**Description:** cells spherical or rounded-pyramidal, rarely united in a common mucilaginous matrix, containing one large parietal, plate-like chloroplast, 2–6 µm in diameter; endospores formed in groups of 4, tetrahedrally divided, 1–3 µm in diameter.

**Remarks:** Ott (2009) listed seven species of *Cyanidium* but most of them had been previously transferred to *Galdieria* (Albertano et al. 2000).

**Representative sequences in GenBank:** AY541298 (*rbcL*).

**Habitat:** the species is most often reported in thermal waters with temperatures of 32–56 °C and low pH (0.5–4.5) and less often in caves with lower temperatures (15–25 °C) and circumneutral pH 7.0–7.2 (Ciniglia et al. 2004; Pinto et al. 2010).

**Distribution:** Asia: Indonesia, Japan; Europe: Italy, Spain (Fig. 2.3).

**Key references:** Geitler (1934), Merola et al. (1981), Albertano et al. (2000).

**Family Galdieriaceae** Merola, Castaldo, De Luca, Gambardella, A Musacchio and Taddei, Giorn Bot Ital 115:193 (1981)

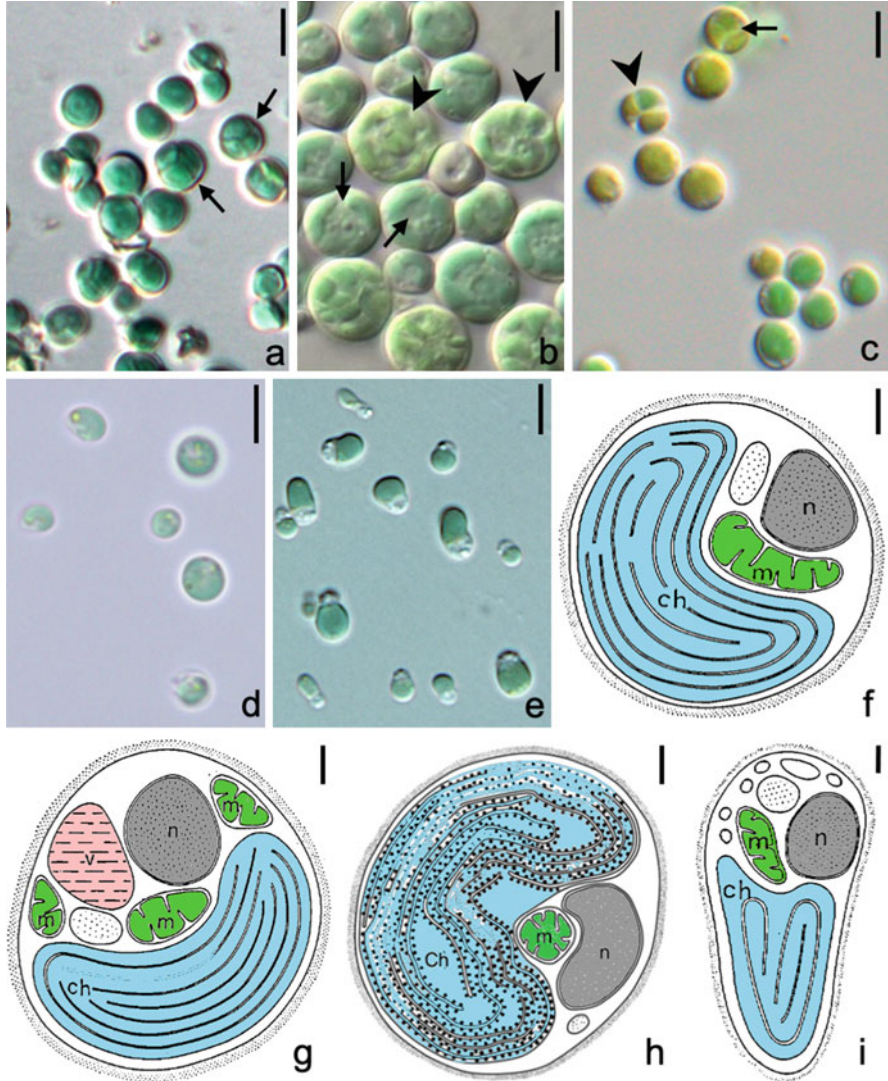
**Description:** cells with multi-lobed chloroplasts, more than one mitochondrion and large vacuoles. Although the genus *Galdieria* Merola has recently been treated as having more than one species, only one species has been widely accepted in the genus.

*Galdieria sulphuraria* (Galdieri) Merola, Giorn Bot Ital 115:193 (1981) (Fig. 2.2b, c, g)

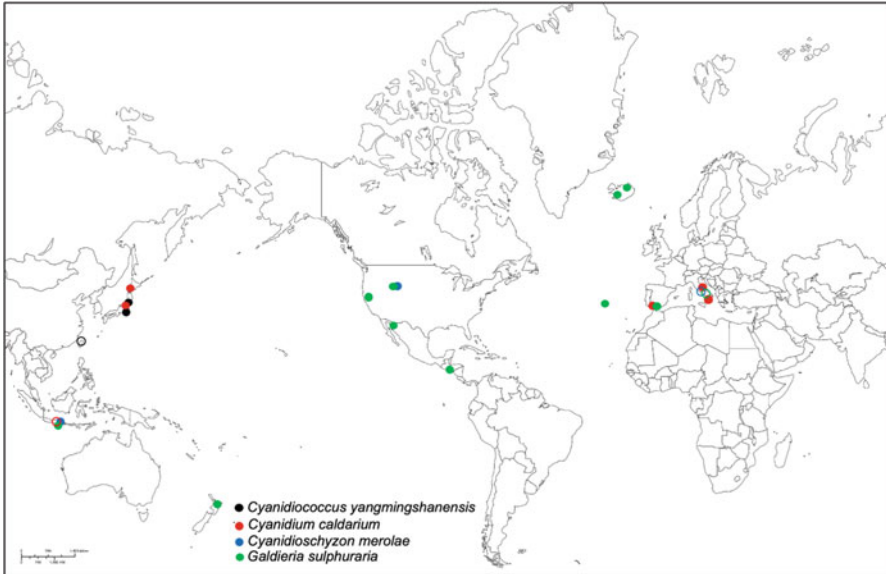
**Basionym:** *Pleurococcus sulphurarius* Galdieri, Atti Reale Accad Sci Fis Mat Napoli, ser. 3 5:162 (1899).

**Type:** NAP, P De Luca, and R Taddei (Neotype); corresponds to strain 002 of the Algal Collection University Federico II (ACUF), Naples, Italy.

**Type locality:** Italy, Naples, Campi Flegrei, Pisciarelli Sulphatare, 40.828244° N, 14.135010° E.



**Fig. 2.2** (a) *Cyanidium caldarium*: (a) spherical cells with endospores (arrows); (b, c) *Galdieria sulphuraria*: (b) spherical cells with vacuoles (arrows) and multi-lobed chloroplasts (arrowheads); (c) spherical cells with vacuole (arrow) and endospores (arrowhead); (d) *Cyanidiococcus yangmingshanensis*: spherical cells; (e) *Cyanidioschyzon merolae*: clavate or ovoidal cells; (f–i) schematic drawing of the main ultrastructural characteristics of the cell: *ch* chloroplast, *m* mitochondria, *n* nucleus, *v* vacuole; (f) *Cyanidium caldarium*; (g) *Galdieria sulphuraria*; (h) *Cyanidiococcus yangmingshanensis*; (i) *Cyanidioschyzon merolae*. Scale bars: (a–e) = 5  $\mu\text{m}$ ; (f–i) = 0.5  $\mu\text{m}$  (Image authors: Fig. (a) M Aboal; Fig. (b) K Mozaffari; Fig. (c) T Leya for Fraunhofer IZI-BB (Strain CCCryo 127-00); Fig. (d) H-Y Fu; Fig. (e) NBRP-Algae (National BioResource Project, Japan, Strain NIES-1332); Fig. (f, g, i) modified from Merola et al. (1981); Fig. (h) modified from Liu et al. (2020))



**Fig. 2.3** World map showing the distribution of *Cyanidiococcus yangmingshanensis*, *Cyanidium caldarium*, *Cyanidioschyzon merolae*, and *Galdieria sulphuraria*. Open symbols represent the type localities

**Description:** cells spherical, sometimes united in a common mucilaginous matrix, containing one parietal, multi-lobed chloroplast, 3–11  $\mu\text{m}$  in diameter; each cell has one to several vacuoles; endospores formed in groups of 2–32.

**Representative sequences in GenBank:** AY541311 (*rbcL*).

**Habitat:** this alga has been reported on humic soils, pools, or streams at very low pH (0–4.5) and variable temperatures (18–55  $^{\circ}\text{C}$ ) (Ciniglia et al. 2004; Pinto et al. 2010; Ciniglia et al. 2014).

**Distribution:** Asia: Indonesia; Europe: Iceland, Italy, Portugal (Azores), Spain; North America: Guatemala, Mexico, the USA (Fig. 2.3).

**Key references:** Merola et al. (1981), Albertano et al. (2000).

**Remarks:** although several species have been accepted in the genus, most are of uncertain taxonomic status and were transferred from the genus *Cyanidium* (Albertano et al. 2000), whereas some are recognized only from molecular data (e.g., *G. phlegrea*, Pinto et al. 2010). We followed Liu et al. (2020) who stated that *G. maxima*, *G. partita*, and *G. daedala* should be treated as invalid names since only cultures of these three species were designated as types. They should be regarded as practical but invalid descriptions. The genus warrants a full revision which is out of scope of this book. Thus, only the type species is treated here.

**Order Cyanidioschyzonales** FD Ott, Handbook of the taxonomic names of non-marine Rhodophycophyta:577 (2009)

**Description:** cells clavate, with nucleus, mitochondrion, and vacuoles positioned at one end; chloroplasts ovoidal or clavate; spores not formed and vegetative reproduction by the formation of two to four daughter cells.

**Family Cyanidioschyzonaceae** FD Ott, Handbook of the taxonomic names of non-marine Rhodophycophyta:578 (2009).

The family had initially only the genus *Cyanidioschyzon* but the recently described *Cyanidiococcus* is shown to have a high similarity of genome structure and closely related phylogenetically justifying its classification in the family. Thus, the family description has to be expanded to include the characteristics of *Cyanidiococcus*. Three species of *Cyanidioschyzon* are known but only one was formally described (Ott 2009), and *Cyanidiococcus* is monospecific (Liu et al. 2020).

*Cyanidiococcus yangmingshanensis* S-L Liu, Y-R Chiang, HS Yoon, and H-Y Fu, J Phycol 56:1435 (2020) (Fig. 2.2d, h)

**Type:** HAST 144519, P-C Chen, 20.i.2015 (Holotype); HAST 144520–144522, TUNG THAL066-001-003 (Isotypes); corresponds to strain THAL066 of the Culture Collection at the Tunghai University, Taichung, Taiwan.

**Type locality:** Taiwan, Yangmingshan National Park, GengZiPing, 25.188333° N, 121.614722° E.

**Description:** cells sub-spherical or short rod-shaped, sometimes united in a common mucilaginous matrix, containing one parietal, polymorphic chloroplast, 1.2–3.8 µm in diameter; reproduction by 2–4 endospores.

**Representative sequences in GenBank:** MN431657 (chloroplast genome).

**Habitat:** the species can inhabit acidic geothermal microhabitats (pH 0.4–5) including pools, hot springs, streams, sulfur fumes, and endoliths.

**Distribution:** Asia: Japan, Taiwan (Fig. 2.3).

**Key references:** Liu et al. (2020).

*Cyanidioschyzon merolae* De Luca, Taddei and Varano, Webbia 33:43 (1978) (Fig. 2.2e, i)

**Type:** NAP, P De Luca (Holotype); corresponds to strain 199 of the Algal Collection University Federico II (ACUF), Naples, Italy.

**Type locality:** Italy, Naples, Campi Flegrei, 40.827000° N, 14.139000° E.

**Description:** cells clavate or ovoidal, with one elongate, polymorphic chloroplast, at one side of the cell, 3–4 µm in length, 1–2 µm in diameter; reproduction by binary fission that occurs longitudinally forming a V-shaped dividing cell.

**Representative sequences in GenBank:** AY541296 (*rbcL*).



**Habitat:** this species has been reported from thermal aquatic habitats in very acidic waters (pH 0–3) and usually high temperatures ( $\geq 32$  °C and up to 55 °C) (Ciniglia et al. 2004; Pinto et al. 2010).

**Distribution:** Asia: Indonesia; Europe: Italy; North America: the USA (Fig. 2.3).

**Key references:** De Lucca et al. (1978), Albertano et al. (2000)

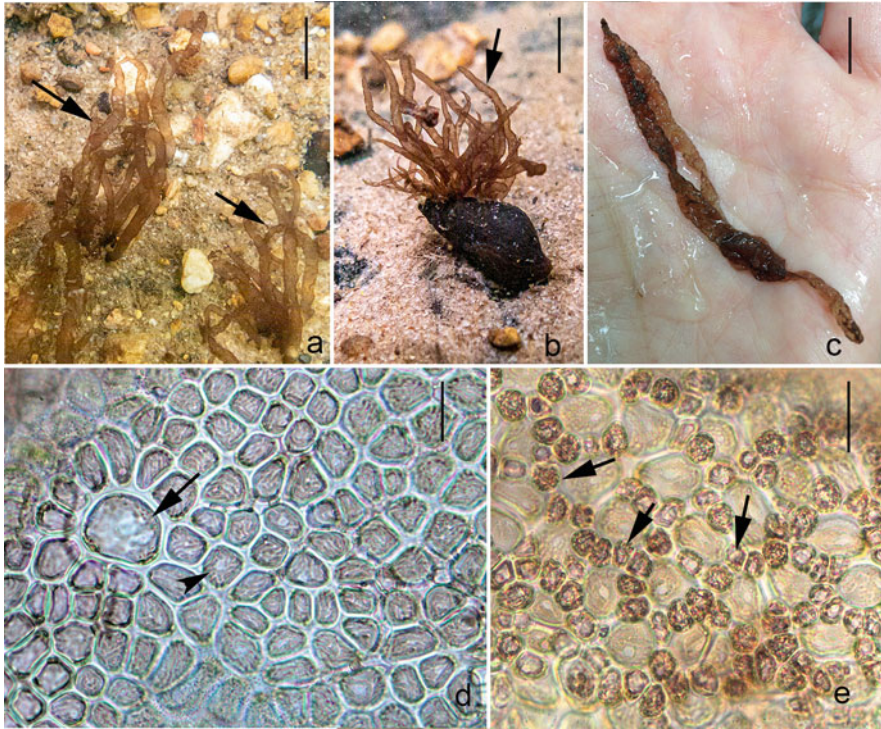
**Subphylum: Proteorhodophytina; SA Muñoz-Gómez, FG Mejía-Franco, K Durnin, M Colp, CJ Grisdale, JM Archibald, and CH Slamovits, *Curr Biol* 27:1680 (2017)**

The characteristics of the subphylum are as follows (adapted from Muñoz-Gómez et al. 2017): red algae with unicellular, pseudofilamentous or filamentous thalli inhabiting mesophilic freshwater and marine environments. Members of this group do not develop macroscopic, pseudoparenchymatous, or parenchymatous seaweed-type thalli as those of the Eurhodophytina; variable plastid morphologies and organellar associations; plastid genomes with a large number of introns and a quadripartite organization in which the rRNA operon-containing inverted repeats are divergent relative to the small single copy region.

This group encompasses four classes (Compsopogonophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae) with the largest plastid genomes sequenced (up to 1,127,474 bp). Within the subphylum two well-supported sister groups were detected, one with the classes Compsopogonophyceae and Porphyridiophyceae and another with the classes Stylonematophyceae and Rhodellophyceae. All four classes occur in freshwater.

***Class: Compsopogonophyceae; GW Saunders and Hommersand, *Am J Bot* 91:1503 (2004)***

Thalli filamentous, crustose, saccate or foliose, macroscopic or microscopic; sometimes with simple pit plugs (only plug core) between cells (*Compsopogon* and *Rhodochaete*); cells covered by cell wall; basically uninucleate. Chloroplasts variable in shape and number, blue-green, violet, or reddish, with peripheral thylakoid; phycobilisomes with allophycocyanin, phycocyanin, and phycoerythrin; with  $\beta$ -carotene, zeaxanthin, and antheraxanthin. Mitochondrion with flat cristae. Asexual reproduction by monospores generated by the oblique asymmetric division of vegetative cells. Sexual reproduction by oogamy (spermatia and carpogonia) and haplodiplontic life cycle reported in some species. Marine or freshwater. Description adapted from Nakayama and Yokoyama (2017). Freshwater members only in the order Compsopogonales.



**Fig. 2.4** (a–e) *Boldia erythrosiphon*: (a) saccate translucent thalli (arrows) in clusters on rock surface; (b) numerous thalli (arrow) growing attached to one end of a snail; (c) collapsed tube-like thalli with dark red or light pink appearance; (d) thallus surface with enlarged clear cell (arrow) and isodiametric (arrowhead) cells having ribbon-shaped chloroplasts; (e) monosporangia (arrows) scattered in chain on the thallus surface. Scale bars: (a–c) = 1 cm; (d, e) 20  $\mu$ m (Image author: Fig. (a, b) SA Krueger-Hadfield)

### Order Compsopogonales Skuja, Acta Horti Bot Univ Latv 11/12:34 (1939)

Thalli mostly macroscopic, filamentous, or saccate, with prostrate filamentous holdfast. Chloroplasts parietal, discoid or ribbon-shaped, lobed, without pyrenoid. Sexual reproduction unknown. Asexual reproduction by monosporangia. Mostly in freshwater streams or lakes, rarely in brackish water. Description adapted from Nakayama and Yokoyama (2017). Members of Compsopogonales are currently classified into two families: Boldiaceae and Compsopogonaceae.

#### Family Boldiaceae Herndon, Am J Bot 51:575 (1964)

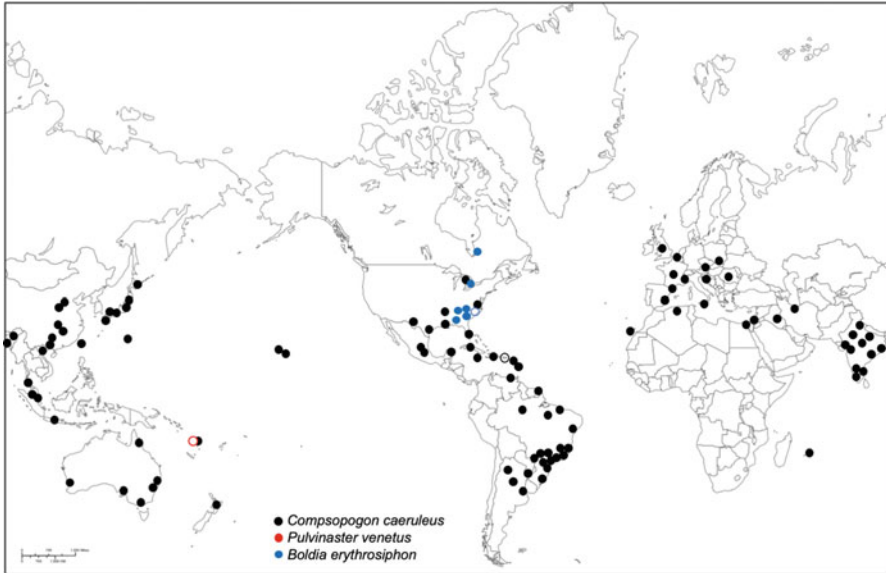
Thalli monostromatic saccate to tubular, reddish, no pit plug.

**Genus *Boldia*** Herndon, Am J Bot 51:575 (1964).

The genus is monospecific and the characters are described below.

***Boldia erythrosiphon*** Herndon, Am J Bot 51:576 (1964) (Fig. 2.4a–e)





**Fig. 2.5** World map showing the distribution of *Boldia erythrosiphon*, *Compsopogon caeruleus*, and *Pulvinaster venetus*. Open symbols represent the type localities

**Synonyms:** *Boldia angustata* Deason and Nichols, J Phycol 6:40 (1970)

**Type:** US, WR Herndon, 05.vii. 1958, (Holotype, not found).

**Type locality:** USA: Virginia, Giles County, near Pembroke, Big Walker Creek, 37.315520° N, 80.643938° W (estimated).

**Description:** Thalli hollow, monostromatic sac attached to surfaces by a disc of cells, 1–20(–75) cm in height and 0.1–2 cm in diameter. Vegetative cells primarily circular, sometimes polygonal to rectangular in surface view, 5–20(–45)  $\mu\text{m}$ , depending on timing of cell division; chloroplasts discoidal or ribbon-shaped; larger, granular ovoidal cells scattered throughout the thallus, 25–40  $\mu\text{m}$  in diameter; monosporangia derived from intercalary filaments, forming a network of cells, polygonal to ovoid, deeply pigmented, 5–9  $\mu\text{m}$  in diameter; monospores germinate to form a disc of cells becoming a cushion-like mound that perennially produces the saccate thalli. No sexual reproduction known.

**Representative sequences in GenBank:** AF087121, AF087122 (*rbcL*).

**Habitat:** in the southern part of the distributional range, this alga often occurs on Pleuroceridae snails as well as attached to rock surfaces, but only epilithic in the northern part of the range. Stream conditions for this alga have been reported to be 6.1–8.5 pH, 3–71  $\text{cm s}^{-1}$  current velocity, low to moderate specific conductance (18–290  $\mu\text{S cm}^{-1}$ ) and a wide range in water temperature 12–25 °C (Sheath and Vis 2015 and references therein). It has often been noted to co-occur with other freshwater red algal taxa of the order Batrachospermales.

**Distribution:** North America: southeastern US and Canada in Ontario and Quebec (Fig. 2.5).

**Key references:** Herndon (1964), Howard and Parker (1980), Sheath and Hymes (1980), Sheath et al. (1989), Sheath and Vis (2015).

**Family Compsopogonaceae** F Schmitz, Natürl Pflanzenfam:318 (1896)

Branched filaments, blue-green to violet, sometimes with pit plugs. Two monospecific genera are currently recognized in the family (*Compsopogon* Montagne and *Pulvinaster* JA West, Zuccarello and JL Scott) and described below.

*Compsopogon caeruleus* (Balbis ex C Agardh) Montagne, Flore d'Algérie, Cryptogamie:154 (1846) (Fig. 2.6a–g)

**Basionym:** *Conferva caerulea* Balbis ex C Agardh, Systema Algarum:122 (1824).

**Synonyms:** listed by Necchi and Dip (1992), Vis et al. (1992), Rintoul et al. (1999), Sheath and Sherwood (2011), and Necchi et al. (2013) including all other species and infraspecific taxa described in the genera *Compsopogon* and *Compsopogonopsis*.

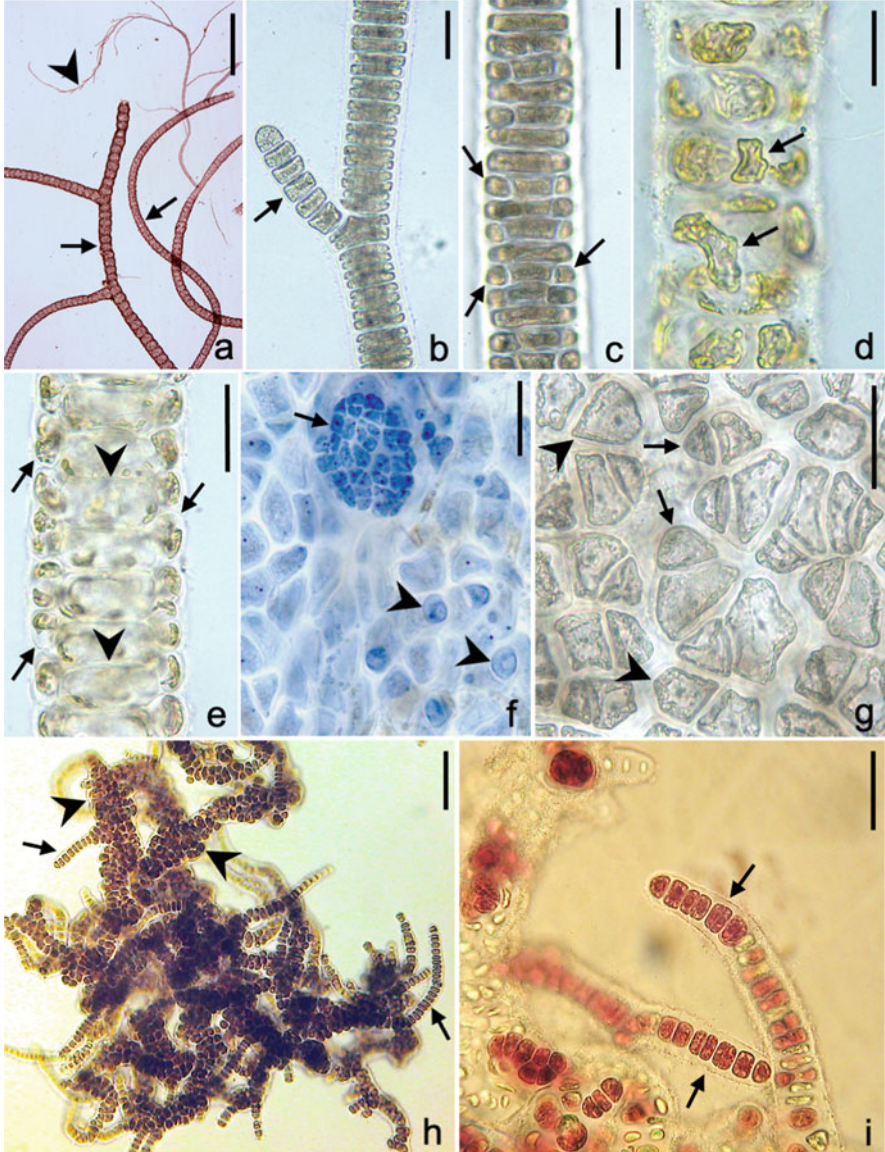
**Type:** LD, Bertero, 23.vii.1824, in Herbarium AGARDH Nr. 12400 (Holotype, not found); PC0047796, PC0047797 (Isotypes).

**Type locality:** Puerto Rico, locality not specified.

**Description:** Thalli heterotrichous, attached by discoid holdfasts, uniseriate rhizoids or knot-like structures; basal system with 1–15 erect branches; spine-like branchlets occasionally produced, irregularly distributed in basal or middle portions. Main axes alternately, rarely unilaterally branched, at variable angles, 30–60(–90°), 100–2000(–3000) µm in diameter. Axial cells barrel-shaped or sub-spherical 45–450 µm in diameter, 50–400 µm in length; axial cells may break down with age leaving the thallus hollow or saccate-like. Cortex consisting of 1–4(–5) cell layers, 15–200(–380) µm in thick; cortication formed by vertical and regular or oblique and irregular divisions of axial cells forming or not rhizoidal filaments; outer cortical cells polygonal, tri- to hexangular or sub-circular in surface view, (10–)15–55(–75) µm in length, (5–)15–30(–40) µm in diameter. Uniseriate branches with disc-shaped or cubic cells, (5–)10–40(–55) µm in diameter, (4–)7–20(–30) µm in length; terminal cells dome-shaped or conical. Monosporangia variable in shape, elliptical, ovoidal, sub-circular, tri- to pentangular or fusiform in surface view, (10–)15–25 (32.5) µm in length, (7.5–)10–20 µm in diameter. Microsporangia occur occasionally, arranged in sori, variable in shape, tri- to pentangular, ovoid or fusiform, 5–12.5 µm in length, 2.5–10 µm in diameter; microsporangial sori irregular in shape, circular, ovoid, square or polygonal in surface view, with (4–)8–35 microsporangia, (10–)40–100(–180) µm in diameter.

**Representative sequences in GenBank:** JX028177, JX028179, JX028186 (COI-5P); JX028155, JX028161, JX028167 (*rbcL*).

**Habitat:** this species has a wide tolerance of environmental variables ranging from clean to moderately polluted waters, slightly acidic to alkaline (pH 6.4–8.3), low



**Fig. 2.6** (a–g) *Compsopogon caeruleus*: (a) general view with corticated (arrows) and uniseriate (arrowhead) filaments; (b) uniseriate filament with a young branch (arrow); (c) filament in early stage of cortication with vertical and regular divisions (arrows); (d) filament in early stage of cortication with oblique and irregular divisions forming rhizoidal cells (arrows); (e) corticated filament with axial cells (arrowheads) and one layer of cortical cells (arrows); (f) surface view of a corticated filament with monosporangia (arrowheads) and microsporangia (arrows); (g) surface view of a corticated filament with monosporangia (arrowheads) and cortical cells (arrows); (h, i) *Pulvinaster venetus*: (h) general view with uniseriate (arrows) and multiserial filaments. (i) apices (arrows) of uniseriate filaments. Scale bars: (a) = 500 µm; (c, f–h) 50 µm; (b, d, e, i) = 25 µm (Image author: Fig. (h, i) JA West)

ion concentrations up to brackish waters (18–1766  $\mu\text{S cm}^{-1}$ ) and mid to high temperatures (most records  $\geq 20^\circ\text{C}$ ) (Necchi et al. 2013 and references therein). This wide ecological niche most likely contributes the ubiquitous distribution of *Compsopogon* in tropical–subtropical regions. It is a warm water species and the few records in temperate locations were at outflows of industries with warm water discharges.

**Distribution:** worldwide in tropical or sub-tropical regions, rarely in temperate areas (Fig. 2.5).

**Key references:** Necchi and Dip (1992), Vis et al. (1992), Rintoul et al. (1999), Eloranta et al. (2011), Necchi et al. (2013).

**Remarks:** Necchi et al. (2013) found little genetic variation based on a global sampling (25 specimens from locations in North America, South America, Europe, Asia, Australasia, and Oceania) for two markers (*rbcL* and COI-5P). They concluded from molecular and morphological evidence that there is only a single monospecific genus worldwide; the oldest specific epithet is *C. caeruleus* and all other species described in the genera *Compsopogon* and *Compsopogonopsis* to be treated as synonyms. This taxon is commonly referred to as “staghorn” algae in the aquarium trade.

***Pulvinaster venetus*** JA West, Zuccarello and JL Scott, Phycologia 46:478 (2007b) (Fig. 2.6h, i)

**Type:** NSW 732559, J West, 14.vi.2005 (Holotype).

**Type locality:** Vanuatu, Efate, Eton River, near a bridge 50 m from the river mouth, 17.733322° S, 168.550023° E.

**Description:** thallus consisting of a prostrate cushion up to 500  $\mu\text{m}$  in diameter, of uniseriate branched filaments, formed by quadrate to ovate cells (9–14  $\mu\text{m}$  in diameter), uninucleate, with a bluish-green parietal lobed or spiral plastid lacking a pyrenoid; older filaments in culture have a thick matrix and are bi- or multiseriate, with up to 25  $\mu\text{m}$  in diameter; sometimes forming unattached branched filaments with elongate cells, 30–55 in length, 8–10  $\mu\text{m}$  in diameter. Reproduction by monosporangia successively formed from lateral branch cells or by gelatinization of cell walls of a thallus sector; monospores spherical, 6–10  $\mu\text{m}$  in diameter, showing a gliding movement. Golgi associated with endoplasmic reticulum; plastid with peripheral thylakoid; no pit connections between derivative cells; low molecular weight carbohydrate floridoside.

**Representative sequences in GenBank:** EF079964 (SSU rDNA); EF079965 (psbA).

**Distribution:** Pacific Islands: Vanuatu (Fig 2.5).

**Habitat:** Epiphytic on red macroalgae (*Bostrychia* and *Caloglossa*) in a shallow, slow-moving, freshwater stream ( $\pm 2$  psi).

**Key references:** West et al. (2007a, b).

**Remarks:** this taxon was invalidly published as *Pulvinus venetus* (West et al. 2007a) and later validated (West et al. 2007b) by referring to the Latin description and figures.

***Class: Porphyridiophyceae; M Shameel, Pakistan J  
Mar Biol:240 (2001)***

Thalli unicellular, sometimes united in a common mucilage. Cells usually exhibiting a gliding movement; uninucleate. Chloroplasts blue-green, green or reddish, without peripheral thylakoid, single, axial, stellate, without or with a naked pyrenoid; phycobilisomes with allophycocyanin, phycocyanin, and usually phycoerythrin; with  $\beta$ -carotene and zeaxanthin. Mitochondrion with tubular cristae. Asexual reproduction by binary fission. Sexual reproduction unknown. Marine, freshwater, or moist soils. Description adapted from Nakayama and Yokoyama (2017). Members of Porphyridiophyceae are currently classified in a single order (**Porphyridiales** Kylin) and family (**Porphyridiaceae** Kylin) with freshwater members in the genera *Flintiella* and *Porphyridium*.

**Genus *Flintiella*** FD Ott in Bourrelly, *Algues D'Eau Douce* 3:194 (1970)

The genus is monospecific and the characters are described below.

***Flintiella sanguinaria*** Ott in Bourrelly, *Algues D'Eau Douce* 3:194 (1970)  
(Fig. 2.7a, b)

**Type:** FD Ott, xi.1964 (Holotype, not found).

**Type locality:** USA, Texas, Travis County, Austin, Barton Springs, 30.264546° N, 97.769241° W.

**Description:** unicellular, spherical, slightly ovoidal prior to division, surrounded by a non-laminated mucilaginous sheath, 6–20(–45)  $\mu\text{m}$  in diameter, with a central nucleus, a single parietal, irregularly and deeply lobed reddish chloroplast without pyrenoid.

**Diagnostic characters:** *Flintiella* can be differentiated from *Porphyridium* by the shape of chloroplast (parietal and lobed versus axial and stellate) and the absence of pyrenoid.

**Representative sequences in GenBank:** AY119774 (*rbcL*).

**Distribution:** North America: the USA (Fig 2.8).

**Habitat:** this alga was collected from the mouth of a spring where it appeared as a pink-colored growth on pebbles in rapidly flowing water with temperature (23–24 °C), pH (6.9), high hardness (301  $\text{mg L}^{-1}$   $\text{CaCO}_3$ ).

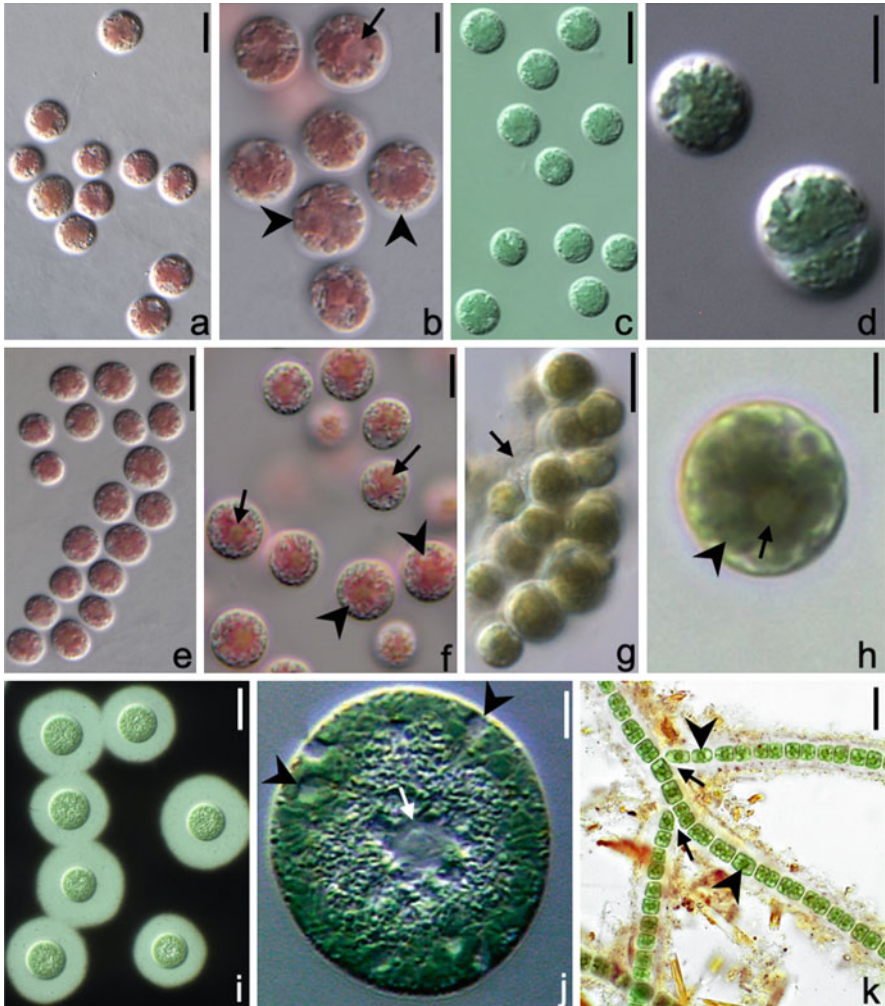
**Key references:** Bourrelly (1970), Ott (1976).

**Genus *Porphyridium*** Nägeli, *Neue Denksch Allg Schweiz Gesellsch Gesamnten Naturwiss* 10:71 (1849)

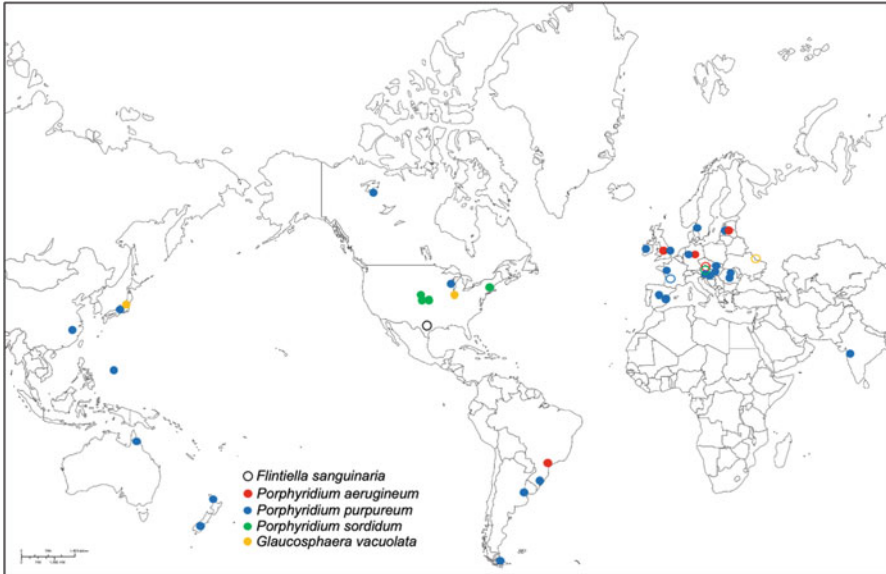
**Description:** unicellular, but often grouped into irregular colonies with an ill-defined mucilaginous matrix, spherical, ellipsoidal, or ovoidal, with a stellate chloroplast and prominent central pyrenoid. Reproduction by cell division; sexual reproduction unknown.

**Diagnostic characters:** *Porphyridium* is characterized by having stellate chloroplasts with a central embedded pyrenoid. Diagnostic characters to recognize





**Fig. 2.7** (a, b) *Flintiella sanguinaria*: (a) group of cells; (b) detail of cells showing nucleus (arrow) and lobed chloroplast (arrowheads); (c-d) *Porphyridium aeruginseum*: (c) group of cells; (d) detail of cells; (e, f) *Porphyridium purpureum*: (e) group of cells; (f) detail of cells showing pyrenoids (arrows) and stellate chloroplasts (arrowheads); (g, h) *Porphyridium sordidum*: (g) colony with cells embedded in a thin mucilage (arrow); (h) detail of a cell showing pyrenoid (arrow) and stellate chloroplast (arrowhead); (i, j) *Glaucosphaera vacuolata*: (i) group of cells surrounded by a mucilage (viewed with China ink); (j) detail of a cell showing nucleus (arrow) and vacuoles (arrowheads); (k) *Chroodactylon ornatum*: (k) pseudofilament with branches (arrows) and cells with pyrenoids (arrowheads). Scale bars: (i, k) = 20  $\mu\text{m}$ ; (a, c, e, g) 10  $\mu\text{m}$ ; (b, d, f) = 5  $\mu\text{m}$ ; (h, j) 2.5  $\mu\text{m}$  (Image author: Fig. (a, b, e-f) T Darienko (SAG Culture Collection of Algae, Goettingen University, Germany; © SAG); Fig. (c) T Friedl (SAG Culture Collection of Algae, Goettingen University, Germany; © SAG); Fig. (d) A Kryvenda (SAG Culture Collection of Algae, Goettingen University, Germany; © SAG); Fig. (g) CCAP (Culture Collection of Algae and Protozoa, Scottish Marine Institute, Scotland); Fig. (h) CCMP (Culture Collection of Algae, Bigelow Laboratory for Ocean Sciences, USA); Fig. (i, j) JA West; Fig. (k, l) C Carter)



**Fig. 2.8** World map showing the distribution of *Flintiella sanguinaria*, *Porphyridium aerugineum*, *P. purpureum*, *P. sordidum*, and *Glaucosphaera vacuolata*. Open symbols represent the type localities

species are essentially based on color, reflecting distinct proportions of phycobiliproteins (allophycocyanin, phycocyanin, and phycoerythrin).

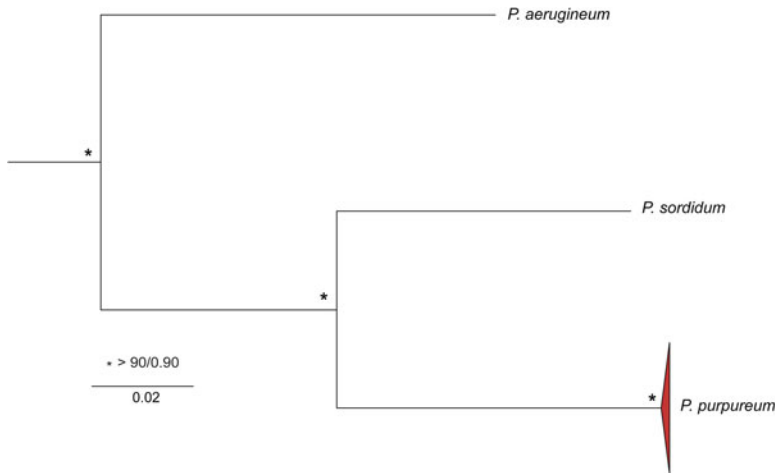
**Habitat:** species are freshwater, marine or occur on moist soils.

**Distribution:** most records are from Europe with some sparse and fragmentary reports for other continents (Fig. 2.8). According to Nakayama and Yokoyama (2017), the distribution of red microalgae is poorly documented and the reported distribution is just the region studied by experts in many cases.

**Phylogenetic relationships among species:** analyses of published *rbcL* sequences (Fig. 2.9) shows two single specimen branches and one clade within the genus *Porphyridium* representing three species: *P. aerugineum*, *P. purpureum*, and *P. sordidum*. The intraspecific variation for *P. purpureum* is low (0.2%).

Key to the species of *Porphyridium*

1a	Cells reddish	<i>P. purpureum</i>
1a	Cells greenish-blue or greenish	2
2a	Cells greenish	<i>P. sordidum</i>
2b	Cells blue-greenish	<i>P. aerugineum</i>



**Fig. 2.9** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the three species of *Porphyridium*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

***Porphyridium aeruginum*** Geitler, Öst Bot Z 72:84 (1923) (Fig. 2.7c, d)

**Type:** not found.

**Type locality:** Austria, Vienna, Vienna University Botanic Garden, 48.191671° N, 16.383968° E (estimated).

**Description:** unicells spherical or ellipsoidal, blue-green, 4.4–8.5(–10.6) µm in diameter.

**Representative sequences in GenBank:** AY119775, X17597 (*rbcL*).

**Distribution:** Europe: Austria, Germany, Great Britain, Latvia; South America: Brazil (Fig 2.8).

**Habitat:** on moist soils or epiphytic on macrophytes in ponds and rivers.

**Key references:** Geitler (1923), Ott (1972, 1987), Pekárková et al. (1989), Eloranta et al. (2011).

***Porphyridium purpureum*** (Bory) KM Drew and R Ross, Taxon 14:98 (1965) (Fig. 2.7e, f)

**Basionym:** *Phytoconis purpurea* Bory, Mémoire sur les genres *Conferva* et *Byssus*:55 (1797).

**Type:** PC0112173, Bory Saint-Vincent (Holotype).

**Type locality:** France, locality not specified.

**Description:** unicells, spherical, blood-red to brownish red, 6.9–12(–15) µm in diameter.

**Representative sequences in GenBank:** DQ308439, MN539012 (*rbcL*).

**Distribution:** Asia: China, India, Japan; Australasia: Australia, New Zealand; Europe: Croatia, France, Germany, Great Britain, Ireland, Hungary, Latvia, Romania, Slovakia, Slovenia, Spain, Sweden; North America: Canada, the USA; Pacific Islands: Micronesia; South America: Argentina, Brazil, Chile (Fig. 2.8).



**Habitat:** on moist terrestrial areas (soil, walls), particularly with calcareous components, brickwork in shaded areas or intermittently submerged in nutrient-rich rivers.

**Key references:** Ott (1972, 1987), Eloranta et al. (2011), Medina-Cabrera et al. (2020).

*Porphyridium sordidum* Geitler, Arch Protistenk 76:603 (1932) Fig. 2.7g, h

**Type:** not found.

**Type locality:** Austria, Pinggau, Steiermark, 47.445564° N, 16.066464° E (estimated).

**Description:** cells spherical or ovoidal, greenish (gray-green, olive-green, or yellow-green), 5.5–9.5(–11.5) µm in diameter.

**Representative sequences in GenBank:** DQ308440 (*rbcL*).

**Distribution:** Europe: Austria; North America: the USA (Connecticut, Iowa, Kansas, Massachusetts, Missouri, Nebraska) (Fig 2.8).

**Habitat:** on moist terrestrial areas (soil, walls), particularly with calcareous components, brickwork in shaded areas or intermittently submerged in nutrient-rich rivers.

**Key references:** Geitler (1932), Ott (1987), Eloranta et al. (2011), Medina-Cabrera et al. (2020).

**Doubtful Species:** A fourth species of *Porphyridium* (*P. griseum* Geitler) has been recognized in some general treatments (Kumano 2002; Eloranta et al. 2011). However, there is no molecular or morphological evidence to support the recognition of this species. It is described as having grayish cells, but this could be only a variation within the color spectrum of other species, particularly *P. sordidum* that could have gray-green cells. Thus, we decided to place it provisionally as a doubtful species until further information is provided to define its taxonomic status.

## ***Class Rhodellophyceae***

Thallus unicellular, sometimes united in a common mucilage. Cells covered by an indistinct cell wall with copious mucilage; uninucleate. Chloroplasts blue-green to reddish, with peripheral thylakoid, axial, stellate to highly lobed, usually with pyrenoid; phycobilisomes with allophycocyanin, phycocyanin and usually phycoerythrin; with β-carotene and zeaxanthin. Mitochondrion with flat cristae. Asexual reproduction by binary fission; sexual reproduction unknown. Most marine, rarely in freshwater. Members of Rhodellophyceae are currently classified into three orders with the only freshwater member in Glaucosphaerales, characterized by a highly lobed peripheral blue-green chloroplast containing no phycoerythrin and without pyrenoid. Description adapted from Nakayama and Yokoyama (2017).

**Genus *Glaucosphaera*** A Korshikov, Arch Protistenk 70:222 (1930)

The genus is monospecific and the characters are described below.

***Glaucosphaera vacuolata*** A Korshikov, Arch Protistenk 70:222 (1930). Fig. 2.7i, j

**Type:** not found.

**Type locality:** Ukraine, Kharkiv, 49.993500° N, 36.230383° E (estimated).

**Description:** cells spherical, 18–25 µm in diameter with a central nucleus, a single highly lobed, blue-green chloroplast, and numerous small vesicles visible throughout the cell; reproduction by binary fission.

**Representative sequences in GenBank:** DQ308427 (*rbcL*).

**Distribution:** Europe: Ukraine; Asia: Japan; North America: the USA (Fig. 2.8).

**Habitat:** this species is a minor component of phytoplankton in ponds; most reports refer to material isolated in culture.

**Key references:** Korshikov (1930), Wilson et al. (2006).

**Class: *Stylonematophyceae*; HS Yoon, KM Müller, Sheath, FD Ott, and D Bhattacharya, J Phycol 42:490 (2006b)**

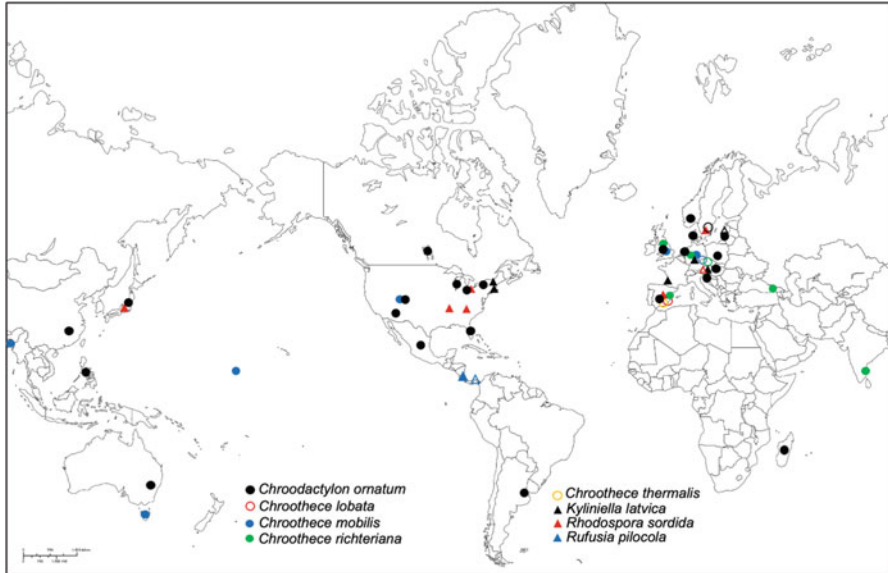
Thalli pseudofilamentous (uniseriate, multiseriate, or tubular), but some are unicellular, mostly microscopic. Cells covered by cell wall and copious mucilage; uninucleate. Chloroplasts blue-green to reddish, with peripheral thylakoid, stellate or discoid, sometimes with pyrenoid; phycobilisomes with allophycocyanin, phycocyanin, and usually phycoerythrin; with β-carotene and zeaxanthin. Mitochondrion with flat cristae. Asexual reproduction by fragmentation, archeospores, endospores (autospores), or binary fission; sexual reproduction unknown for most members, but spermatia and carpogonia reported in *Kylinella*. Most marine but some in freshwater. Description adapted from Nakayama and Yokoyama (2017). Members of Stylonematophyceae are currently classified into two orders: Rufusiales and Stylonematales.

**Order Stylonematales** KM Drew, Bot Tidsskr 22:73 (1956)

Thalli pseudofilamentous or unicellular; cells with an axial stellate chloroplast containing pyrenoid or parietal chloroplast without pyrenoid. Description adapted from Nakayama and Yokoyama (2017). There is only one family (**Stylonemataceae** Drew) with the same characters of the order. Four genera occur in freshwater.

Key to the genera of Stylonematales

1a	Cells with several parietal, discoid chloroplasts, without pyrenoid	2
1b	Cells with one axial, stellate chloroplast, with one pyrenoid	3
2a	Unicells, sometimes forming colonies	<i>Rhodospira</i>
2b	Unbranched pseudofilaments	<i>Kyliniella</i>
3a	Cells arranged in long pseudofilaments	<i>Chroodactylon</i>
3b	Cells solitary, less often forming short pseudofilaments	<i>Chroothece</i>



**Fig. 2.10** World map showing the distribution of *Chroodactylon ornatum*, *Chroothoece lobata*, *C. mobilis*, *C. richteriana*, *C. thermalis*, *Kyliniella latvica*, *Rhodospora sordida*, and *Rufusia pilicola*. Open symbols represent the type localities

**Genus *Chroodactylon*** Hansgirg, Ber Deutsch Bot Ges 3:14 (1885)

**Type species:** *Chroodactylon wolleanum* Hansgirg, Ber Deutsch Bot Ges 3: 14 (1885).

**Description:** pseudofilaments with false branching or unbranched, encircled in a broad, mucilaginous sheath with an irregular and uniseriate arrangement; cells sub-spherical to ellipsoidal, containing one blue-green, stellate, axial chloroplast, with a prominent pyrenoid. Reproduction by monosporangia and fragmentation. Sexual reproduction unknown.

**Diagnostic characters:** this genus is differentiated from others based on pseudofilaments with false branching and a large blue-green, stellate chloroplast with prominent pyrenoid; however, see discussion of *Chroothoece* as this genus may also produce short pseudofilaments.

**Habitat:** primarily epiphytic on macroalgae in marine, brackish and freshwaters.

**Distribution:** this genus has been reported from marine and brackish coastal waters of North and South America, Asia, and Europe; it is widespread in alkaline freshwaters on numerous continents (Fig. 2.10).

**Remarks:** the number of species that should be recognized in this genus is unclear. There are three validly published and currently taxonomically accepted species (*C. depressum*, *C. ornatum*, and *C. wolleanum*); however, most modern freshwater treatments (e.g., Eloranta et al. 2011, Sheath and Vis, 2015) only recognize one species, *C. ornatum* and this scheme will be followed here. More research on the morphology and DNA sequence data is needed for this genus.

***Chroodactylon ornatum*** (C Agardh) Basson, Bot Mar 22:67 (1979) (Fig. 2.7k)

**Type:** LD A1863, C Agardh (Holotype).

**Type locality:** Sweden, near Stockholm, Lake Mälaren, Bridge near Transberg, 59.446679° N, 17.466347° E (estimated).

**Description:** pseudofilaments with 0–6 false branches, 0.024–10 mm in length; cells sub-spherical to ellipsoidal, 7.1–16.6 µm in length, 5.8–11.6 µm in diameter, containing one blue-green, stellate, axial chloroplast, with a prominent pyrenoid.

**Representative sequences in GenBank:** DQ308429, EF660259, EF7660260 (*rbcL*).

**Distribution:** Africa: Madagascar; Asia: China, Japan, Philippines; Australasia: Australia; Europe: Austria, Croatia, Denmark, Hungary, Lithuania, Netherlands, Norway, Poland, Slovak Republic, Spain, Sweden, Switzerland, UK; North America: Canada, Mexico, USA; South America: Argentina (Fig 2.10).

**Habitat:** growing as an epiphyte on aquatic plants and macroalgae, especially *Cladophora*; typically, in alkaline waters with pH 7.5–8.5 and conductivity 170–540 µS cm<sup>-1</sup>. This taxon has been reported in large streams, but more often in lakes; in North America, it occurs as a common epiphyte of *Cladophora* in the Great Lakes.

**Key references:** Vis and Sheath (1993), Eloranta et al. (2011)

**Remarks:** DNA sequence data available in GenBank are from North America, Philippines and Madagascar and differ by 1.1–1.8% suggesting that more research may be warranted to circumscribe the species and its geographic range.

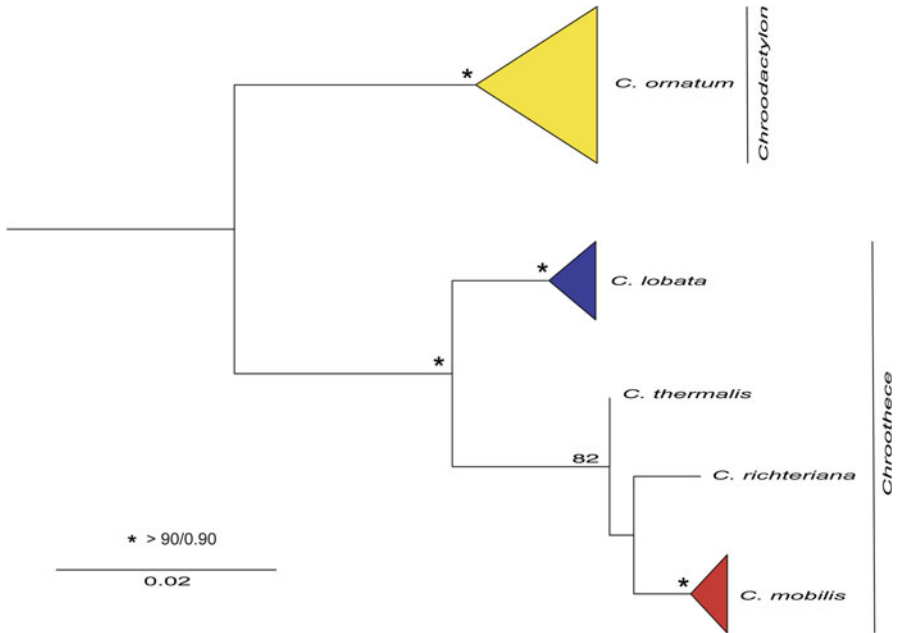
**Genus *Chroothoece*** Hansgirg, Öst Bot Zeit 34:353 (1884)

**Type species:** *Chroothoece richteriana* Hansgirg in Wittrock and Nordstedt, Bot. Not. 1884:128 (1884).

**Description:** cells solitary or joined pole to pole, less often forming short pseudofilaments, immersed in a firm and stratified mucilaginous matrix, the basal pole extending into a lamellated stalk; cells ellipsoidal to cylindrical, containing one blue-green, stellate, axial chloroplast, with a prominent pyrenoid. Reproduction by cell division and by fragmentation. Sexual reproduction unknown.

**Diagnostic characters:** *Chroothoece* is morphologically similar to *Chroodactylon* and they are typically separated by cell arrangement (Eloranta et al. 2011; Necchi 2016): unicells or small colonies in *Chroothoece* and pseudofilaments in *Chroodactylon*. However, short pseudofilaments, branched or unbranched, are often observed in *Chroothoece* species in culture and sometimes in the field (Aboal et al. 2018). Thus, there is overlap but the pseudofilaments are typically shorter in *Chroothoece* in comparison to *Chroodactylon* and the two genera are clearly distinct based on *rbcL* sequences. More research is needed to determine if there are other morphological characters to separate these genera.

**Habitat:** species are mostly aerophytic within permanent seeps over different types of rocks or less often aquatic. *Chroothoece mobilis* is reported as both aerophytic on limestones with permanent seepage and low irradiance (Aboal et al. 2018) or



**Fig. 2.11** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the four species of *Chroothoece* and *Chroodactylon ornatum*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

aquatic at pH 7.2–7.8, temperature 13° C and conductivity 340–570  $\mu\text{S cm}^{-1}$  (Blinn and Prescott 1976). *Chroothoece lobata* is found aquatic in calcareous and slightly saline water: temperature 11.4–28.8°C, pH 8.0–8.9, conductivity 281–3100  $\mu\text{S cm}^{-1}$  and *C. richteriana* at temperature 11.9–22.3°C, conductivity 2640–3100  $\mu\text{S cm}^{-1}$ , oxygen 8.3–10.4  $\text{mg L}^{-1}$  (Aboal et al. 2014, 2018). *Chroothoece thermalis* occurs in a thermal spring (temperature 38° C) on detrital rock above water level (Aboal et al. 2018).

**Distribution:** one species (*C. mobilis*) is relatively widespread, whereas *C. richteriana* is mostly reported from Europe and two species (*C. lobata* and *C. thermalis*) are endemic, restricted to the type localities in Spain (Fig. 2.10).

**Phylogenetic relationships among species:** analyses of *rbcL* sequences from data reported by Aboal et al. (2018) supports recognition of *Chroothoece* as a distinct genus forming a clearly separated clade from *Chroodactylon* (Fig. 2.11). *Chroothoece* has two high-supported major clades: one with two sequences of *C. lobata* from Spain and another with sequences of three species (*C. mobilis*, *C. richteriana*, and *C. thermalis*) from distinct regions of the world.

Key to the species of *Chroothecce*

1a	Mean cell diameter $\leq 10 \mu\text{m}$	<i>C. richteriana</i>
1b	Mean cell diameter $\geq 10 \mu\text{m}$	2
2a	Mean cell diameter $\leq 14 \mu\text{m}$ , colonies lobed	<i>C. lobata</i>
2b	Mean cell diameter $\geq 14 \mu\text{m}$ , colonies forming mats	3
3a	Aquatic in thermal spring (38° C)	<i>C. thermalis</i>
3b	Aerophytic on cave wall or aquatic in cool waters (13° C)	<i>C. mobilis</i>

***Chroothecce lobata*** Aboal, BA Whitton, IS Chapuis, P Sánchez, and Necchi, Eur J Phycol 53:194 (2018) (Fig. 2.12a, b)

**Type:** MUB-ALGAE-2076, I Chapuis, P Sánchez and M Aboal, 14.ii.2014 (Holotype); GDA-A-6332 (Isotype).

**Type locality:** Spain, Murcia, Umbria, River Chícamo, 38.265316° N, 0.991772° W.

**Description:** colonies hemispherical or lobate, blue-green to yellow-orange; pseudofilaments of 3–4 cells frequent, occasionally branched; cells ellipsoidal, 11–31.1  $\mu\text{m}$  in length, 7–14(–17.4)  $\mu\text{m}$  in diameter; mucilaginous sheath 1.2–2.2  $\mu\text{m}$  thick, smooth.

**Representative sequences in GenBank:** KY962002, KY962005 (*rbcL*).

**Distribution:** Europe: Spain (Fig 2.10).

**Key references:** Aboal et al. (2018).

***Chroothecce mobilis*** Pascher and J Petrová, Arch Protistenk 74:490 (1933) (Fig. 2.12c, d)

**Type:** not found.

**Type locality:** Czech Republic, Bohemia, Franzensbad, 50.120059° N, 12.349681° E (estimated).

**Description:** Colonies forming a mat, blue-green to yellow-orange; pseudofilaments frequent, up to 5 cells, with short branches; cells ellipsoidal, (23.5–)28.5–38.5(–45)  $\mu\text{m}$  in length, 15.4–22.5(–27)  $\mu\text{m}$  in diameter; mucilaginous sheath 1.6–3–6.6  $\mu\text{m}$  thick, smooth.

**Representative sequences in GenBank:** DQ308430, KY962004 (*rbcL*).

**Distribution:** Asia: Bangladesh; Australasia: Australia; Europe: Czech Republic, Germany, Great Britain, Spain; North America: the USA; Pacific Islands: Guam (Fig. 2.10).

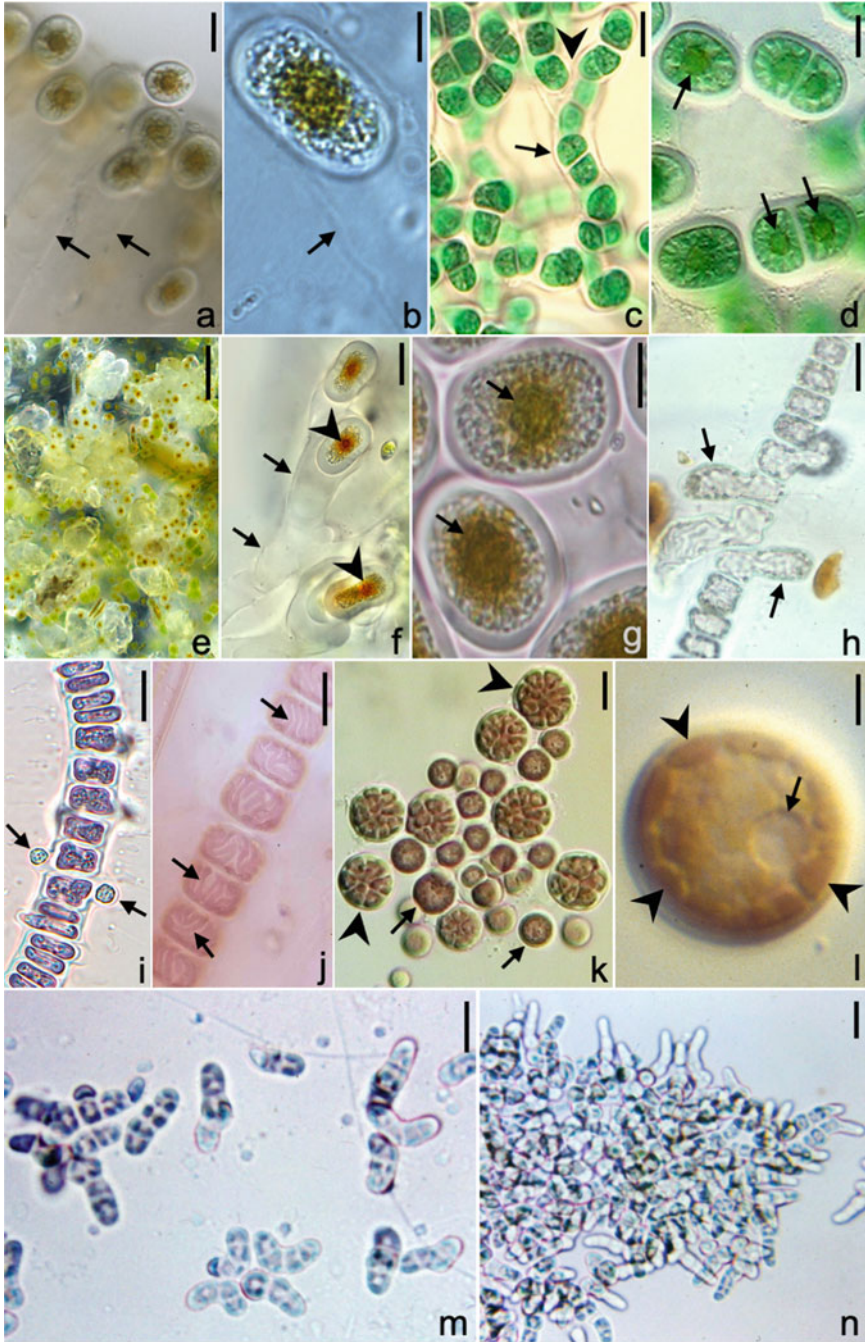
**Key references:** Pascher and Petrová (1933), Blinn and Prescott (1976), Eloranta et al. (2011), Aboal et al. (2018).

***Chroothecce richteriana*** Hansgirg, Öst Bot Zeit 34:353 (1884) (Fig. 2.12e, f)

**Type:** not found.

**Type locality:** Czech Republic, Bohemia, Auzitz near Kralup, 50.241645° N, 14.310645° E (estimated).





**Fig. 2.12** (a, b) *Chrootheca lobata*: (a) colony with stalks; (b) detail of cell showing stalk (arrow); (c, d) *Chrootheca mobilis*: (c) colony with pseudofilament (arrow) and branch (arrowhead); (d) detail of cells with stellate chloroplasts and pyrenoids (arrows); (e, f) *Chrootheca richteriana*: (e) general view of the mat in the field; (f) colony with stalks (arrows) and cells with pyrenoids (arrowheads)

**Description:** Colonies forming a mat or hemispheric, blue-green when young and brownish, yellowish, or orange with age; pseudofilaments not observed; cells ellipsoidal, 15–33  $\mu\text{m}$  in length, 5–10  $\mu\text{m}$  in diameter; mucilaginous sheath 2–4  $\mu\text{m}$  thick, layered.

**Representative sequences in GenBank:** KY962003 (*rbcL*).

**Distribution:** Europe: Czech Republic, Germany, Great Britain, Russia, Spain; Asia: India (Fig. 2.10).

**Key references:** Eloranta et al. (2011), Aboal et al. (2014, 2018).

*Chroothoece thermalis* IS Chapuis, P Sánchez, Aboal, and Necchi, Eur J Phycol 53: 195 (2018) (Fig. 2.12g)

**Type:** GDA 6334, I Chapuis, 26.x.2012 (Holotype); MUB-ALGAE 5835 (Isotype).

**Type locality:** Spain: Granada, Santa Fé, 37.157639° N, 3.751861° E.

**Description:** colonies forming a mat, blue-green or yellowish; pseudofilaments not observed; cells cylindrical, (15–)20–29  $\mu\text{m}$  in length, (12–)14–24  $\mu\text{m}$  in diameter; mucilaginous sheath 2.5–4  $\mu\text{m}$  thick, slightly undulated; stalks striated and wavy, transparent.

**Representative sequences in GenBank:** KY962006 (*rbcL*).

**Distribution:** Europe: Spain (Fig 2.10).

**Key references:** Aboal et al. (2018).

**Genus *Kylieniella*** Skuja, Acta Hort Bot Univ Latvi 1:4 (1926)

The genus is monospecific and the characters are described below.

*Kylieniella latvica* Skuja, Acta Hort Bot Univ Latvi 1:4 (1926) (Fig. 2.12h–j)

**Type:** S A36450, H Skuja, 20.viii.1926 (Holotype); MICH 660558 (Isotype).

**Type locality:** Latvia, Usma Parish, Lake Usma, 57.160699° N, 22.170287° E (estimated).

**Description:** pseudofilaments unbranched, arising from a discoid and pseudoparenchymatous base, 12–32  $\mu\text{m}$  in diameter; cells discoid or cubic, contiguous, or separate, arranged within a broad mucilaginous sheath; each cell containing several parietal, reddish, discoid, or band-shaped chloroplasts, 4.9–17.5(–22)  $\mu\text{m}$  in length and 7.4–11(–19)  $\mu\text{m}$  in diameter, length/diameter 0.5–1.0; rhizoidal outgrowths occur at points of contact among cells, 17–25(–170)  $\mu\text{m}$  in length, 7–10(–12.5)  $\mu\text{m}$  in diameter. Asexual reproduction by small fragments



**Fig. 2.12** (continued) (*arrowheads*); (**g**) *Chroothoece thermalis*: (**g**) detail of cells with pyrenoids (*arrows*); (**h–j**) *Kylieniella latvica*: (**h**) pseudofilament with rhizoidal outgrowths (*arrows*); (**i**) pseudofilament with monosporangia (*arrows*); (**j**) pseudofilaments with cells showing band-shaped chloroplasts (*arrows*); (**k, l**) *Rhodospira sordida*: (**k**) colony with unicells (*arrows*) and cells with autospores (*arrowheads*); (**l**) cell with nucleus (*arrow*) and discoid chloroplasts (*arrowheads*); (**m, n**) *Rufusia pilicola*: (**m**) young filaments; (**n**) mature filaments. *Scale bars*: (**c, f, n**) = 20  $\mu\text{m}$ ; (**a, d, g–k, m**) 10  $\mu\text{m}$ ; (**b**) = 5  $\mu\text{m}$ ; (**l**) 2.5  $\mu\text{m}$  (Image author: Fig. (**a–c, g, j**) M Aboal; Fig. (**d, k**) JA West; Fig. (**e, f**) C Carter; Fig. (**l**) J Johansen; Fig. (**m, n**) D Wujek)



(hormogonia) and monosporangia released from the sheath. Presumptive sexual reproduction with small colorless spermatia and large, pigmented carpogonia with tubular projections. Postfertilization structures unknown.

**Representative sequences in GenBank:** DQ30843 (*rbcL*).

**Distribution:** Europe: Austria, France, Germany, Latvia, Sweden; North America: northeastern United States (Rhode Island and New Hampshire) (Fig 2.10).

**Habitat:** this taxon has few records and is an epiphyte on macrophytes and macroalgae; in North America, it is a rare component in the littoral zone of soft water streams (Sheath and Vis 2015); in Europe, it is reported associated with macrophytes in hardwater streams with temperature 4.7–9.4° C, conductivity 515–785  $\mu\text{S cm}^{-1}$ , and pH 8.2–8.5 (García-Fernández et al. 2012).

**Key references:** Skuja (1926), Vis and Sheath (1993), Eloranta et al. (2011), García-Fernández et al. (2012).

**Genus *Rhodospora*** Geitler, Öst Bot Zeit 76:28 (1927)

The genus is monospecific and the characters are described below.

***Rhodospora sordida*** Geitler, Öst Bot Zeit 76:28 (1927) (Fig. 2.12k, l)

**Type:** not found.

**Type locality:** Austria, Salzburg, Bad Gastein, 47.114089° N, 13.132661° E (estimated).

**Description:** unicells 4.5–18  $\mu\text{m}$  in diameter, sometimes united into irregular colonies within a mucilaginous matrix which may be layered; each cell with several parietal, discoid, red-violet, olive-green or yellow chloroplasts; reproduction by cell division and formation of 4–32 autospores. Sexual reproduction unknown.

**Representative sequences in GenBank:** DQ308433 (*rbcL*).

**Distribution:** Asia: Japan; Europe: Austria, Spain, Sweden; North America: the USA (Arkansas, Tennessee, Ohio) (Fig 2.10).

**Habitat:** this taxon has few records and is an epiphyte on macrophytes and macroalgae.

**Key references:** Geitler (1927), Johansen et al. (2005), Eloranta et al. (2011).

**Order Rufusiales** Zuccarello and JA West, J Phycol 44:392 (2008)

Thalli consisting of branched pseudofilaments; cells with several red to violet, parietal discoid to band-shaped chloroplasts without pyrenoid; asexual reproduction by fragmentation or by many endospores per cell; found on the hair of sloths.

The order is monotypic with a single genus and species that are described below.

The order has only one family (**Rufusiaceae** Zuccarello and West) with a single genus (*Rufusia* Wujek and Timpano).

***Rufusia pilicola*** Wujek and Timpano, Brenesia 25/26:165 (1986) (Fig. 2.12m, n)

**Type:** figures 1–4, page 168 in Wujek and Timpano (1986, Holotype).

**Type locality:** Panama, Barro Colorado Island, 9.150722° N, 79.846437° W (estimated).

**Description:** vegetative cells barrel-shaped or short-cylindrical, 5.5–10 µm in diameter and 3.5–10 µm in length; mature reproductive cells 10–15 µm in diameter; endospores 1.5–2 µm in diameter.

**Representative sequences in GenBank:** DQ308435 (*rbcL*); DQ308455 (*psaA*).

**Distribution:** North America—Costa Rica, Panama (Fig 2.10).

**Habitat:** this alga grows within fissures and furrows of the hair of three-toed (*Bradypus*) and two-toed (*Choloepus*) sloths.

**Key references:** Wujek and Timpano (1986), Zuccarello et al. (2008).

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# Chapter 3

## Subphylum Eurhodophytina, Classes Bangiophyceae and Florideophyceae, Subclasses Corallinophycidae, Hildenbrandiophycidae, and Rhodymeniophycidae



Orlando Necchi Jr and Morgan L Vis

**Abstract** Subphylum Eurhodophytina is classified into two classes: Bangiophyceae and Florideophyceae. Class Bangiophyceae has a single order Bangiales, which is divided into two families: Bangiaceae with the type genus, *Bangia*, and a single species *Bangia atropurpurea* as the only occurring in freshwaters; and Granulifilaceae with the monospecific type genus, *Granulifilum rivularis* exclusively of freshwaters. Class Florideophyceae has several subclasses and those treated in this chapter are: Corallinophycidae, Hildenbrandiophycidae, and Rhodymeniophycidae. Corallinophycidae has only one species in freshwaters (*Pneophyllum cetinaensis*). Hildenbrandiophycidae has marine and freshwater members, and three species have been recognized in freshwater (*Hildenbrandia angolensis*, *H. jigongshanensis*, and *H. rivularis*). Rhodymeniophycidae has freshwater representatives in two orders: Ceramiales with three genera: *Bostrychia* (seven species), *Caloglossa* (six species), and *Polysiphonia* (one species); Gigartinales with the single genus *Sterrocladia* (two species).

**Keywords** Bangiophyceae · Ceramiales · Corallinophycidae · Florideophyceae · Freshwater · Gigartinales · Hildenbrandiophycidae · Rhodophyta · Rhodymeniophycidae · Taxonomy

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**Class: Bangiophyceae; Wettstein, Handbuch der systematischen Botanik. Vol. 1: 187 (1901)**

The characteristics of the class are as follows (adapted from Lindstrom 2017): life history heteromorphic; haploid gametophyte foliose, with 1–2 cell layers thick or an unbranched cylindrical filament or uniseriate to multiseriate cells; cells with one, rarely two (or more) stellate chloroplasts with a central pyrenoid; growth parenchymatous; pit plugs lacking; spermatangia produced by division of cell contents into packets; the released spermatia fertilizing slightly differentiated female cells, which divide into packets of zygotosporangia; zygotospores germinating to form the diploid sporophyte (the branched, uniseriate, filamentous “conchocelis” phase), which can bore into shells; cells of the “conchocelis” are short cylindrical, with discoid chloroplasts lacking pyrenoids, connected by a pit plug with a single cap layer, and with apical growth; reproduction by differentiated cells called conchospores; meiosis thought to occur upon germination of the conchospore; young gametophytes have bipolar germination, producing basal rhizoids and an upright filament; both phases repeated by asexual spores in some species.

The class Bangiophyceae contains a single order Bangiales, which is divided into two families: the Bangiaceae, which is primarily composed of marine members (except the type genus) and the Granulifilaceae with a single monospecific genus occurring exclusively in freshwaters (Zhao 1995; Shi et al. 2006).

**Order Bangiales** Nägeli, Neue Denk Allg Schw Ges Gesamten 9(2):136, 252 (1847)

Same characters as the class.

**Family Bangiaceae** DUBY, Aug. Pyrami de Candolle Botanicon gallicum sen synopsis plantarum in flora gallica descriptarum:16 (1830).

Same characters as the order. The genus *Bangia* Lyngbye is the only genus occurring in freshwaters, and it is currently exclusive of freshwater habitats.

*Bangia atropurpurea* (Mertens ex Roth) C Agardh, Systema algarum:76 (1824) (Fig. 3.1a–d)

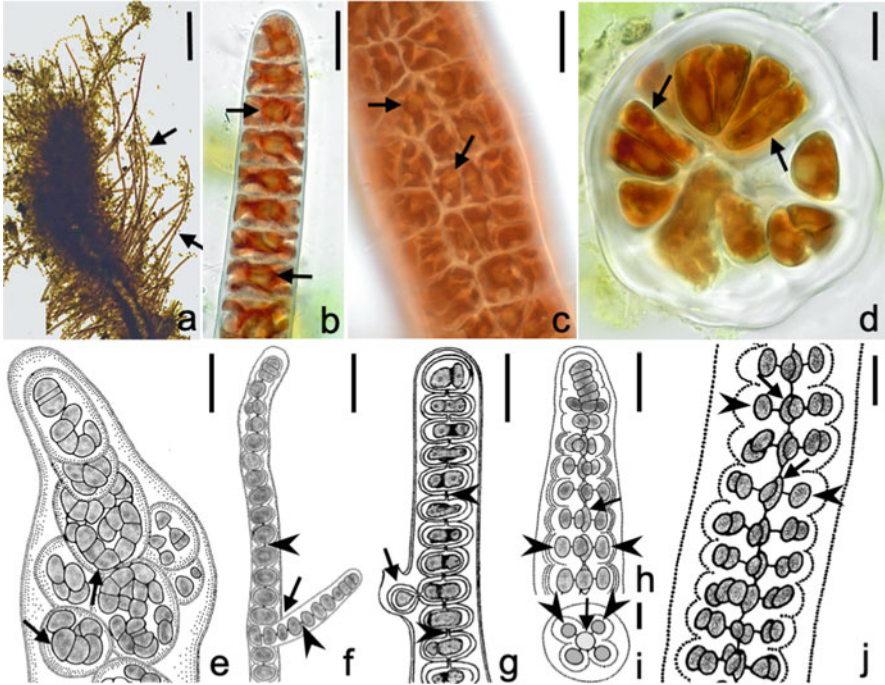
**Basionym:** *Conferva atropurpurea* Mertens ex Roth, Catalecta Botanica:208 (1806).

**Type:** BM 000637980, K Müller and A Sherwood, 24.v.1998 (Neotype, designated by Müller et al. 2003).

**Type locality:** Netherlands, Ysselmeer, Enschede, 52.221537° N, 6.893662° E (estimated).

**Description:** thalli consisting of cylindrical filaments embedded in firm gelatinous matrix, uniseriate or multiseriate, unbranched, attached by down-growing rhizoids produced from basal and adjacent cells; uniseriate filaments, 8–30 µm in diameter, formed by disc-shaped or cubic cells, 13–60 µm in length, 6–15 µm in diameter; multiseriate filaments with cells variable in shape,





**Fig. 3.1** (a–d) *Bangia atropurpurea*: (a) general view of the thalli epiphytic on a green macroalga (*Cladophora*); (b) apex of a uniseriate filament with disc-shaped cells containing one stellate chloroplast and one prominent pyrenoid (arrows); (c) multiserial filament with variable shape cells containing one stellate chloroplast and one prominent pyrenoid (arrows); (d) cross section of a multiserial filament with one layer of cell (arrows); (e–j) *Granulifilum rivularis*: (e) young thallus with short filaments (arrows); (f, g) uniseriate filaments with young branches (arrows) and pit connections (arrowheads); (h) apex of a multiserial filament with axial (arrow) and periaxial (arrowhead) cells; (i) cross section of a multiserial filament with axial (arrow) and periaxial (arrowhead) cells; (j) mid portion of a multiserial filament with axial (arrow) and periaxial (arrowhead) cells. Scale bars: (a) = 250  $\mu\text{m}$ ; (c, e–h) = 25  $\mu\text{m}$ ; (b, d, i–j) = 10  $\mu\text{m}$  (Image author: Fig. (a–d) C Carter; Fig. (e–f, h–j) modified from Shi et al. (2006); Fig. (g) modified from Zhao (1995))

60–380  $\mu\text{m}$  in diameter; cells with a large, axial, stellate chloroplast with one prominent pyrenoid; asexual reproduction usually by monosporangia; sexual populations rarely reported in freshwater, and when observed carpogonia and spermatangia noted.

**Remarks:** although a relatively wide variation in morphology has been reported among freshwater populations worldwide, only one species has been recognized based on DNA sequence data (Müller et al. 1998; Hanyuda et al. 2004).

**Representative sequences in GenBank:** DQ191330 (COI-5P); AB114640, AF169330, DQ408162 (*rbcL*).

**Habitat:** in North America, it has been reported in the Great Lakes, particularly Lakes Ontario, Erie, Huron, Michigan, and connected water bodies Lake Simcoe





**Fig. 3.2** World map showing the distribution of *Bangia atropurpurea* and *Granuifilum rivularis*. Open symbols represent the type localities

and the upper St. Lawrence River, all of which are alkaline (Sheath and Vis 2015); in Europe, it has been reported in alkaline lakes and rivers, mostly near coastal areas, pH 8–8.7, conductivity 37–540  $\mu\text{S cm}^{-1}$  (Sheath and Sherwood 2002; Eloranta et al. 2011).

**Distribution:** Africa: Benin, Egypt, Gabon, Ghana, Morocco, Nigeria, Senegal, South Africa; Asia: China, Cyprus, Iraq, Israel, Japan, Kuwait, Philippines, Russia, South Korea, Taiwan, Tajikistan, Turkey, Vietnam; Europe: Albania, Britain, Bulgaria, Croatia, Cyprus, France, Germany, Hungary, Ireland, Italy, Netherlands, Norway, Portugal (Azores and Madeira), Romania, Slovakia, Slovenia, Spain, Sweden, Turkey; North America: Canada, Greenland, Mexico, the USA; South America: Argentina, Chile, Peru, Uruguay; Australasia: Australia, New Zealand; Pacific Islands: Central Polynesia, Hawaii (Fig. 3.2).

**Key references:** Müller et al. (1998, 2003), Sheath and Sherwood (2002), Eloranta et al. (2011).

**Family Granuifilaceae** Shi, Xie, and Dong, Flora Algarum Sinicarum Aquae Dulcis 13: Rhodophyta, Phaeophyta:30 (2006)

The characteristics of the family are as follows (adapted from Zhao 1995 and Shi et al. 2006): thalli microscopic, filamentous, with true branching, uniseriate in young parts and becoming multiseriate in older parts; filaments grow apically, with central (axial) and pericentral cells, forming pit connections; chloroplasts parietal, plate-like or ring-shaped with 1–3 pyrenoids; asexual reproduction by

monosporangia; sexual reproduction involving spermatangia that are formed directly from vegetative cells and carpogonia that develop directly into carposporangia; gonimoblast filaments absent.

This family was established by Shi et al. (2006) based on the genus *Granuofilum* XF Zhao (1995) and placed in the subclass Florideophycidae, order Nemaliales, family Acrochaetiaaceae. Shi et al. (2006) transferred it to the Bangiales based on similarities of growth mode and differentiation of axial cells and peripheral cells, the sexual reproduction of certain genera (such as *Porphyra* and *Bangia*). A taxonomic approach involving the two freshwater members of the Bangiales are highly recommended including DNA sequence data of *Granuofilum* for a better understanding of the phylogenetic relationship with members of the Bangiaceae and its taxonomic status within the order.

*Granuofilum rivularis* Zhao, Oceanol Limnol Sin 26:431 (1995) *emend.* Shi and Xie, Flora Algae Sinicarum Aquae Dulcis 13: Rhodophyta, Phaeophyta:31 (2006) (Fig. 3.1e–j)

**Type:** WZUH 850403, X Zhao, 29.iv.1985 (Holotype).

**Type locality:** China, Zhejiang Province, Taishun County, Wuyanling, 27.705692° N, 119.675329° E.

**Description:** thalli developing in three different growth forms; young thalli forming a colloid colony by multiple rows of cell filaments, consisting of irregular clumps, composed of thick and layered individual and colony colloids, with cells arranged irregularly or in short filaments; cell shape variable, often ellipsoidal, spherical, or ovoidal, 5–10 µm in length, 4–10 µm in diameter; mature thalli consists of uniseriate filaments embedded in a firm, thick gelatinous matrix, branched, 8–40 µm in diameter, cells ellipsoidal, spherical, ovoidal, or rarely cylindrical, 5–20 µm in length, 6–25 µm in diameter; fully developed thalli multiseriate, branched, 37–70 µm in diameter, composed of axial cells and periaxial cells; axial cells spindle-shaped, 6–8 µm in diameter; periaxial cells ellipsoidal or ovoidal, 8–16 µm in length, 5–10 µm in diameter, often arranged in groups of four, symmetrically and regularly around the axial cells; fan-shaped in cross section.

**Remarks:** sexual reproductive structures need further investigation to describe in more detail and compare with other groups of red algae to determine taxonomic affinities. Thallus structure with axial and periaxial cells resembles the vegetative morphology in the Ceramiales (Rhodomelaceae), whereas the reproductive structures as presently known appear to be quite different and simpler than this order. Thus, a complete reevaluation of the taxonomic position and status of this red alga including DNA sequence data is warranted.

**Representative sequences in GenBank:** no sequences available.

**Habitat:** this species was originally collected in a stream with temperature 18 °C and pH 6 (Zhao 1995), and further collections were made in a subaerial habitat on the surface of dripping rocks (Shi et al. 2006).

**Distribution:** Asia: China (Fig. 3.2).

**Key references:** Zhao (1995), Shi et al. (2006).

**Class: Florideophyceae; Cronquist, Bot Rev 26:437 (1960)**

The characteristics of the class are as follows (adapted from Kamiya 2017): thalli multicellular, essentially filamentous and branched, often united to form pseudoparenchymatous structures, cylindrical, compressed, or foliose, primarily growing from apical meristems; cells uni- or multinucleate, linked by pit connections; pit plug filling pit connection naked or associated with 1 or 2 cap layers and/or cap membranes; life cycle primarily triphasic, isomorphic, or heteromorphic free-living diploid tetrasporophyte and haploid gametophytes, with fully or semi-parasitic carposporophytes dependent on the female gametophytes; gametophytes monoecious or dioecious, reproduction oogamous with non-flagellate male gametes (spermatia), a differentiated filament (carpogonial branch) forming a terminal egg cell (carpogonium) with an elongate extension (trichogyne), fertilization by fusion of spermatium to trichogyne; diploid carposporophyte tissue (gonimoblast) initiated from a fertilized carpogonium or a specialized cell (auxiliary cell) that receives the diploid nucleus directly or indirectly from a fertilized carpogonium; terminal cells or most cells of gonimoblast becoming carposporangia; carpospores develop into diploid tetrasporophytes, which usually form tetrasporangia, in which a tetrad of meiotic tetraspores are produced and zonately, cruciately, or tetrahedrally divided. A variation in typical life cycle with the production of haploid gametophytes by somatic meiosis from diploid sporophyte is present in members of the freshwater red algal orders Batrachospermales and Thoreaales.

The Florideophyceae is the most taxonomically diverse of all red algal groups with ~6750 species, from which ~94% are marine and the others are brackish and/or freshwater. It is closely related to the Bangiophyceae based on features of the reproductive cells, the association of the Golgi apparatus with ER/mitochondria, the formation of pit connections, and the presence of group I introns. The close relationship of these two classes has been supported by molecular phylogenetic analyses. The Florideophyceae is divided into five subclasses, Hildenbrandiophycidae, Nemaliophycidae, Corallinophycidae, Ahnfeltiophycidae, and Rhodymeniophycidae. Ahnfeltiophycidae is the only subclass without representatives in freshwater, whereas the class Nemaliophycidae contains the vast majority of non-marine members, including three orders occurring in exclusively freshwater habitats (Balbianiales, Batrachospermales, and Thoreaales).

***Subclass: Corallinophycidae; L Le Gall and GW Saunders, Mol Phylogenet Evol 43:1129 (2007)***

The characteristics of the subclass are as follows (adapted from Kamiya 2017): thalli calcification by calcite; pit plugs with two cap layers, outer layer domed and cap membrane absent; gametophytes and tetrasporophytes isomorphic; reproductive structures in uniporate or multiporate conceptacles; tetrasporangia zonately or cruciately divided.

**Order Corallinales** PC Silva and HW Johansen, Br Phycol J 21:250 (1986)

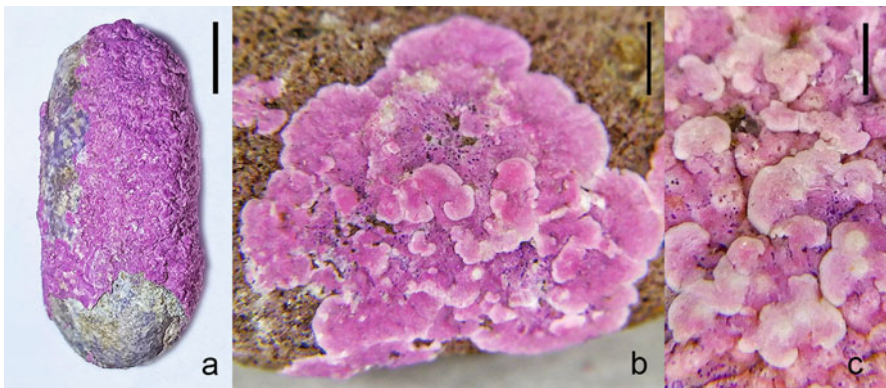
The characteristics of the order are as follows (adapted from Kamiya 2017): thalli either geniculate (jointed) or non-geniculate (crustose), multiaxial, pseudoparenchymatous, or more rarely partly to largely unconsolidated filaments; meristematic cells either terminal, or intercalary; producing one or more epithelial cells with partially calcified walls (inner uncalcified and outer calcified); walls of other vegetative cells calcified; cell fusions or secondary pit connections present between adjacent vegetative filaments. Gametophytes monoecious or dioecious; carpogonia and spermatangia within uniporate conceptacles; apical plugs absent at conceptacle pore. Tetrasporangia zonate, in uniporate or multiporate conceptacles. Meiotic bisporangia sometimes replacing tetrasporangia. There is one family (**Corallinaceae** JV Lamouroux) with the same characteristics of the order.

*Pneophyllum* Kützing, Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange:385 (1843)

**Description:** thalli consisting of thin crusts, 2–3(–5) cells thick, epilithic or epiphytic, adhering by cell adhesion, lack haustoria; two orders of filaments with first-order filaments on substrate and second-order filaments oriented at right angles to the substrate; trichocytes when present, single or in groups; intercalary within first-order filaments and sometimes terminating second-order filaments. Reproductive structures in protruding uniporate conceptacles.

**Remarks:** a single species is known from freshwaters in a unique karst watershed near the marine environment.

*Pneophyllum cetinaensis* S Kaleb, A Žuljević and V Peña, Sci Rep-UK 6:2 (2016) (Fig. 3.3a–c)



**Fig. 3.3** (a–c) *Pneophyllum cetinaensis*: (a) macroscopic view of encrusting thalli attached to rock; (b) pinkish thalli with white margins growing in semi-circular pattern; (c) details of thalli surface; Scale bars: (a) = 1 cm; (b) = 2 mm; (c) = 1 mm (Image author: N Koletić)

**Type:** PC 0145164 A. Žuljević, 27.viii.2013 (Holotype), PC 0145165, PC 0145166, PC 0145167, NHMS 000566, NHMS 000567, NHMS 000568, CNHM 600: ZAG;1:BOA, ZA 39846, ZA 39848 (Isotypes).

**Type Locality:** Croatia: Otok Ljubavi, Cetina River, 43.436408° N, 16.763144° E.

**Description:** thalli pink to violet with white margins, non-geniculate, encrusting or layered, forming crusts up to 60 mm in diameter; gametangial thalli monoecious; male conceptacles uniporate, at or slightly protruding above surrounding thallus surface with chambers conical 83–88 µm in diameter, 24–28 µm in height; female conceptacle uniporate simple, without papillae, slightly raised or hemispherical with domed to elliptical chambers 225–232 µm in diameter, 85–93 µm in height; tetrasporangial conceptacles uniporate, hemispherical and protruding, with elliptical chambers, 130–182 µm in diameter, 60–77 µm in height and a small columella usually present at the base; tetrasporangia zonate 100–110 µm in length, 60–64 µm in diameter.

**Diagnostic characters:** this is the only known freshwater coralline red algal species.

**Representative sequences in GenBank:** KT783425 (*psbA*).

**Distribution:** Europe: Croatia, numerous locations throughout the Cetina River (Fig. 3.12).

**Key References:** Žuljević et al. (2016), Koletić et al. (2020b).

**Remarks:** this species appears to be restricted to a highly specialized calcareous (karstic) freshwater system located adjacent to a marine habitat with high pH (7.7–8.3), conductivity (282–602 µS cm<sup>-1</sup>), and calcium hardness (116–218 mg L<sup>-1</sup> CaCO<sup>-3</sup>).

### ***Subclass: Hildenbrandiophycidae; GW Saunders and M Hommersand, Am J Bot 91:1504 (2004)***

The characteristics of the subclass are as follows (adapted from Gurgel 2017): thalli crustose, with or without erect branches, cartilaginous; surface smooth or tuberculate; structure of the basal layer consisting of laterally adherent branched filaments, with each cell producing an erect, laterally coherent filament of small cuboidal cells; in erect taxa, upright filaments developing a medulla of anastomosing filaments and a cortex of appressed anticlinal filaments; rhizoids absent; primary and secondary pit connections present; pit plugs with a single cap layer and membrane; sexual reproduction unknown; tetrasporangia zonately or irregularly divided, borne in ostiolate conceptacles. One order (**Hildenbrandiales** Pueschel and Cole) and one family (**Hildenbrandiaceae** Rabenhorst) with the same characteristics of the subclass. Between the two genera in the family, *Hildenbrandia* is the only occurring in freshwater but also has marine species.

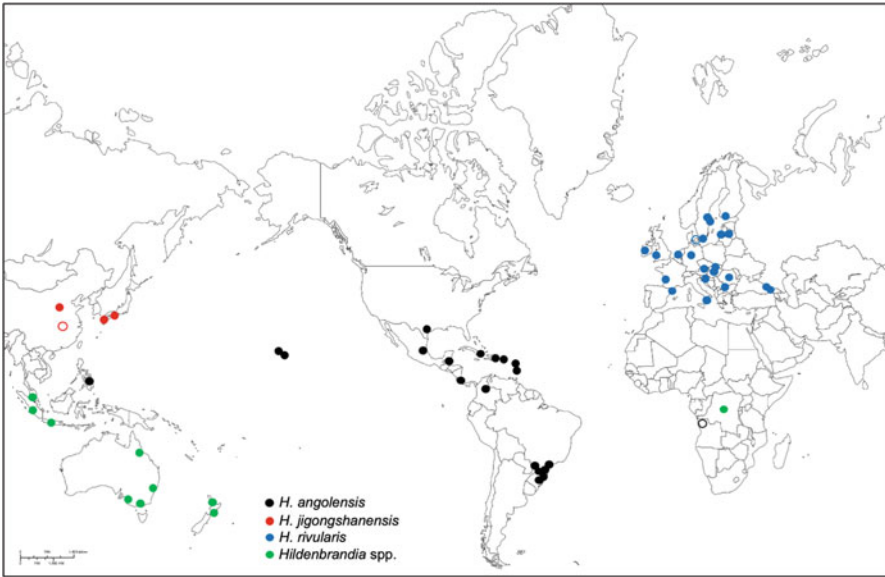
**Genus *Hildenbrandia*** Nardo, Isis von Oken 1834:676 (1834)

**Description:** thalli consisting of crusts forming red patches on rocky substrata; marginal part of the thallus monostromatic, radiating from the center, composed of creeping filaments of cylindrical cells; central part of the thallus multi-stromatic, composed of erect filaments of cubic cells in side view and polygonal in front view; reproduction in freshwater populations exclusively vegetative via fragments, offshoots, and gemmae.

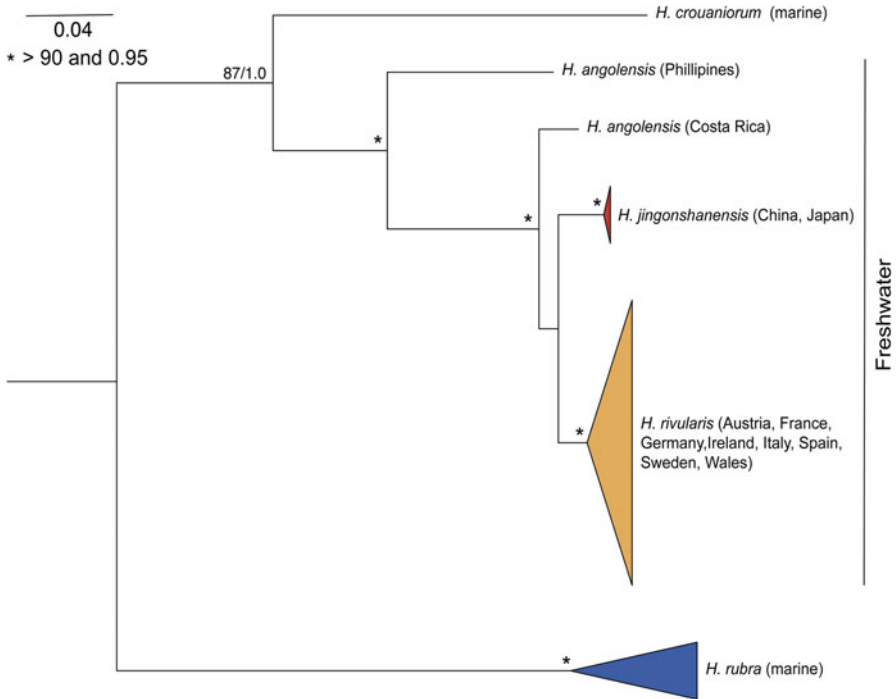
**Habitat:** *H. angolensis* is found in streams, rivers, or cascades with temperature of (11–)14–27 °C, pH (4.8–)6.5–8.6, conductivity (24–)70–1558  $\mu\text{S cm}^{-1}$ , current velocity (5–)30–178  $\text{cm s}^{-1}$ , 2–60 cm in depth and shaded segments (Sheath et al. 1993a, b; Branco et al. 2011). *Hildenbrandia rivularis* is often reported in Europe, where it occurs in streams, rivers, and ponds, on stable rocky surfaces at temperature of 9–18 °C, pH 7.0–8.8, conductivity 56–460  $\mu\text{S cm}^{-1}$ , current velocity (6–)24–100  $\text{cm s}^{-1}$  and shaded segments (Sheath and Sherwood 2002; Eloranta 2019). Environmental data are not available for *H. jigongshanensis* that grows firmly attached on the rock substrate in rapidly flowing streams of a forest area (Nan et al. 2017), a trout farm (Nan et al. 2019) and in three rivers from Japan (Vieira et al. 2021).

**Distribution:** *H. angolensis* has been reported from tropical regions of Africa, North and South America, and Oceanic Islands (Sheath et al. 1993a, b; Sherwood and Sheath 2003; Branco et al. 2011), whereas *H. rivularis* is widely distributed in Europe from Italy in the south to Finland in the north (Sheath et al. 1993a, b; Sheath and Sherwood 2002; Sherwood and Sheath 2003; Eloranta et al. 2011) (Fig. 3.4). *Hildenbrandia jigongshanensis* has been collected in few localities from China and Japan (Nan et al. 2017, 2019; Vieira et al. 2021) (Fig. 3.4). There are several reports to *H. rivularis* from other parts of the world (Fig. 3.4) that are here referred as *Hildenbrandia* spp. because the species occurs only in Europe using the current species concept.

**Phylogenetic relationships among species:** *rbcL* sequences show two clades and two single branches within the genus (Fig. 3.5). One clade represents *H. rivularis* from several locations in Europe, whereas the other is *H. jigongshanensis* from China and Japan. The two single branches represent two samples identified as *H. angolensis*, one from North America (Costa Rica) and the other from Asia (Philippines). The genetic variation indicates that they represent two distinct species; however, which or if either actually represent the species is yet to be determined since the type locality is from Africa (Angola) and no sequence data are available from that continent. The three freshwater species form a well-supported clade, that is clearly separate from two marine species; *H. crouaniorum* is positioned as sister to the freshwater species, whereas *H. rubra* is in a more distant clade. Among the freshwater species, the genetic variation was much higher in *H. rivularis* (0.1–2.1%) than in *H. jigongshanensis* (0–0.9%).



**Fig. 3.4** World map showing the distribution of *H. angolensis*, *H. jigongshanensis* and *H. rivularis*. Open symbols represent the type localities. *Hildenbrandia* spp. refers to locations where the genus has been reported but the species designation is uncertain by the current criteria; these records do not represent the same species but show the wider geographic distribution of the genus



**Fig. 3.5** Phylogenetic tree of the freshwater species of *Hildenbrandia* (*H. angolensis*, *H. jigongshanensis*, and *H. rivularis*) and two marine species (*H. crouaniorum* and *H. rubra*) based on *rbcl* sequences. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities



Key to the freshwater species of *Hildenbrandia*

1a	Erect filaments $\leq 5$ $\mu\text{m}$ mean cell diameter	<i>H. angolensis</i>
1b	Erect filaments $\geq 7$ $\mu\text{m}$ mean cell diameter	2
2a	Known distribution in Asia (China and Japan)	<i>H. jigongshanensis</i>
2b	Known distribution in Europe	<i>H. rivularis</i>

*Hildenbrandia angolensis* Welwitsch ex W West and GS West, J Bot 35: 3 (1897) (Fig. 3.6a–d)

**Type:** BM000530645, BM001039189, FMJ Welwitsch no. 150 (I and II), vi.1857 (Syntypes).

**Type locality:** Angola, Golungo Alto, 9.141283° S, 14.772902° W (estimated).

**Description:** thalli consisting of crusts forming irregular discs, 20–180  $\mu\text{m}$  in thickness, up to 2 cm in diameter; erect filaments with 4–15(–17) cubic or barrel-shaped cells, 18–125  $\mu\text{m}$  in length, cells 3–7(–11)  $\mu\text{m}$  in length, 2–7(–10)  $\mu\text{m}$  in diameter; gemmae (17–)35–150  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinguished from the other two freshwater species by the smaller dimensions of the cells forming the erect filaments. However, the range in cell diameter overlap among the species as previously noted by Sheath et al. (1993a, b), particularly between *H. angolensis* and *H. rivularis*. Therefore, DNA sequence data and geographic distribution should be used to reliably identify these species.

**Representative sequences in GenBank:** AF107817, AF534409 (*rbcL*).

**Distribution:** Africa: Angola; Asia: Philippines; North America: Belize, Costa Rica, Cuba, Dominica, Dominican Republic, Grenada, Guadeloupe, Martinique, Mexico, Puerto Rico, Saint Vincent, the USA; Pacific Islands: Hawaii; South America: Brazil, Colombia (Fig. 3.4).

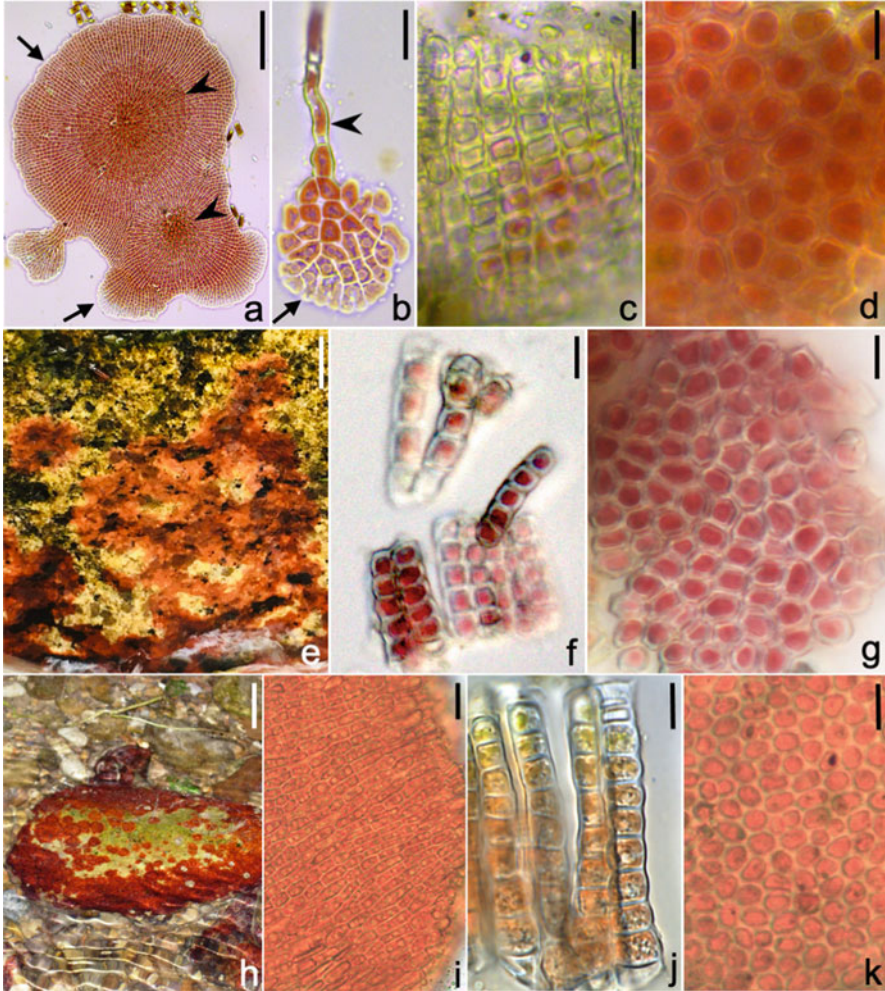
**Key references:** Sheath et al. (1993a, b), Sherwood and Sheath (2003).

**Remarks:** the only sequence data presently available are from North America (Costa Rica) and the other from Asia (Philippines) and show genetic variation indicative of two distinct species. Since neither sequence is from Africa, it is unclear which, if either, represents the “true” *H. angolensis*. For the geographic distribution, all records of *H. angolensis* with enough morphological data to identify to species are presented. This species has been reported from Spain (Ros et al. 1997), but DNA sequences from Spain belong to *H. rivularis*, which is exclusive to Europe.

*Hildenbrandia jigongshanensis* FR Nan and SL Xie, Phytotaxa 292:245 (2017) (Fig. 3.6e–g)

**Type:** SXU- HN15006, F-R Nan, C-Y Gong, H Su, J Feng, and S-L Xie, 28.vii.2015 (Holotype).

**Type locality:** China, Henan Province, Jigongshan Mountain, 31.80° N, 114.07° E.



**Fig. 3.6** (a–d) *Hildenbrandia angolensis*: (a) general view of a young thallus with marginal monostromatic (arrows) and central polystromatic regions (arrowheads); (b) a small gemma (arrow) with a young filament (arrowhead); (c) side view of erect filaments; (d) upper view of erect filaments; (e–g) *H. jigongshanensis*: (e) general view in the natural habitat; (f) side view of erect filaments; (g) upper view of erect filaments; (h–k) *H. rivularis*: (h) general view in the natural habitat; (i) marginal part of thallus with prostrate filaments; (j) side view of erect filaments; (k) upper view of erect filaments. Scale bars: (e, h) = 5 cm; (a) = 100  $\mu\text{m}$ ; (b, c, f, g, i–k) = 10  $\mu\text{m}$ ; (d) = 5  $\mu\text{m}$  (Image authors: Fig. (e–g) C Vieira and S Akita; (h) F Rindi; (i–k) C Carter)

**Description:** thalli consisting of crusts forming thick irregular discs, up to 2 cm in diameter; erect filaments with 7–12 cubic to short-cylindrical cells, 308–491  $\mu\text{m}$  in length, cells (5–)8–15  $\mu\text{m}$  in length, (3–)8–12.5(19.6)  $\mu\text{m}$  in diameter; gemmae not described.

**Diagnostic characters:** this species is distinguished by the larger cell dimensions of the erect filaments although there is some overlap, particularly with *H. rivularis*. Therefore, DNA sequence data and geographic distribution should be used to reliably identify these species.

**Representative sequences in GenBank:** LC565120, LC565125 (*rbcL*).

**Distribution:** Asia: China, Japan (Fig. 3.4).

**Key references:** Nan et al. (2017), Nan et al. (2019).

**Remarks:** Vieira et al. (2021) recently synonymized *H. japonensis* with this species based on similarity of the *rbcL* sequence data and this taxonomic conclusion is followed here.

*Hildenbrandia rivularis* (Liebmann) J Agardh, Species genera et ordines Floridearum, part 2:495 (1851) (Fig. 3.6h–k)

**Basionym:** *Erythroclathrus rivularis* Liebmann, Naturhistorisk Tids 2(bind 1):174 (1938).

**Type:** C-A-17636, vi.1826 (Holotype).

**Type locality:** Denmark, Sealand, Kongens Mølle, 55.640000° N, 11.350000° E (estimated).

**Description:** thalli consisting of crusts forming thin irregular discs, up to 2.5 cm in diameter; erect filaments with (4–)7–12(–16) cubic to barrel-shaped cells, (26–)40–90(–120) µm in length, cells (4.0–)8.7–13 µm in length, (3.5–)5–10(–12) µm in diameter; gemmae 30–100 µm in diameter.

**Diagnostic characters:** this species is distinguished from *H. angolensis* by the larger cell dimensions of the erect filaments although there is some overlap, particularly with *H. jigongshanensis*. Therefore, DNA sequence data and geographic distribution should be used to reliably identify these species.

**Representative sequences in GenBank:** AF208797, AF208804, AF208811(*rbcL*).

**Distribution:** Europe: Austria, Bulgaria, Croatia, Denmark, Finland, France, Georgia, Germany, Great Britain, Hungary, Ireland, Italy, Latvia, Poland, Romania, Slovakia, Slovenia, Spain, Sweden (Fig. 3.4).

**Key references:** Sheath et al. (1993a, b), Sheath and Sherwood (2002), Sherwood and Sheath (2003), Eloranta et al. (2011).

**Remarks:** most reports of freshwater *Hildenbrandia* worldwide are referred to *H. rivularis*. However, the current species concept based on morphological and DNA sequence data indicates that the species is restricted to Europe. Records of this species from other continents may represent other species and are labeled *Hildenbrandia* spp. (Fig. 3.3) to show the genus occurrence in the world.

**Doubtful species:** *Hildenbrandia ramanaginae* M Khan, Hydrobiologia 44:238 (1974)

This species most likely does not belong to the genus *Hildenbrandia*. It has characters that are not present in the genus: olive-green color, erect filaments branched profusely and with lateral branching; *Hildenbrandia* is always reddish, erect filaments are sparsely branched and with dichotomous branching. In

addition, erect filaments [as illustrated in Fig. 2 of the protologue (Khan 1974)] have distinct lengths forming an irregular upper surface, whereas *Hildenbrandia* has erect filaments of the same length, forming a flat and regular upper surface. The taxonomic status of this species requires a review.

***Subclass: Rhodymeniophycidae; GW Saunders and M Hommersand, Am J Bot 91:1504 (2004)***

The characteristics of the subclass are as follows (adapted from Huisman 2017): triphasic life history; carposporophyte developing directly from the fertilized carpogonium or carpogonium fusion cell, or indirectly from an auxiliary cell that received the zygotic diploid nucleus; pit plugs covered by cap membranes, lacking cap layers, except the Gelidiales with inner cap layers; molecular phylogenetic analyses resolved the Rhodymeniophycidae as monophyletic, but the relationships within this subclass need to be resolved. This subclass is poorly represented in freshwater and only a few members of two orders (Ceramiales and Gigartinales) among the 12 are known from non-marine habitats.

**Order Ceramiales** Nägeli, Neue Denksch Allg Schweiz Gesellsch Gesamnten Naturwiss 9: 196 (1847)

The characteristics of the order are as follows (adapted from Huisman 2017): thalli small filamentous tufts to delicate membranous or large foliose thalli; uniaxial; pit plugs lack cap layers; life history triphasic, with isomorphic gametophytes and sporophytes; tetrasporangia tetrahedrally or cruciately divided, borne on whorl branches or lateral branches, occasionally in stichidia; carpogonial branches usually four-celled, arising from a supporting cell (fertile pericentral cell); auxiliary cells arising from a supporting cell usually after fertilization, or the supporting cells acting as auxiliary cells; gonimoblast arising from an auxiliary cell, with or without a basal fusion cell, branched gonimoblast filaments with all cells forming carposporangia; mature carposporophyte naked or covered by a filamentous involucre or pseudoparenchymatous pericarp; spermatangia in spherical or elongate heads, solitary or clustered from cells of whorl branches, occasionally in flat cushions or sorus-like structures.

This group is very diverse and species rich (Huisman 2017) with nine families presently recognized, and freshwater representatives found only in two families: Delesseriaceae (genus *Caloglossa*) and Rhodomelaceae (genera *Bostrychia* and *Polysiphonia*).

**Family Delesseriaceae** Bory, Voyage autour du monde, Botanique, Cryptogamie:181 (1828)

The characteristics of the family can be summarized as follows (adapted from Huisman 2017): triphasic life history, with free-living haploid gametophytes bearing gametangia on the same or separate thalli; vegetative growth primarily initiated by a single, transversely dividing, dome-shaped apical cell; intercalary cell divisions usually absent in the first-order cell rows; midribs associated with rhizoids.

*Caloglossa* G Martens, Flora 52:234 (1869)

**Type Species:** *Caloglossa leprieurii* (Montagne) G Martens, Flora 52:234 (1869)

**Description:** thalli reddish, dichotomously, sub-dichotomously, rarely trichotomously branched, consisting of flat, articulate, narrow leafy segments; prominent midrib evident composed of a broad axial cell, surrounded by two to four periaxial cells, appearing like rows of cylindrical or barrel-shaped cells in surface view; outer portions of the leafy segments monostromatic with oblique series of hexagonal cells, called wing cells; rhizoids and new leafy segments arise at constrictions (nodes), either from the midrib area or peripheral layer of cells; freshwater populations vegetative; reproductive structures unknown.

**Habitat:** freshwater populations may be found in strictly freshwater habitats, but typically occur in river estuaries, mangroves, and similar areas with brackish water. In some locations, they can colonize upstream segments with no salt water influence. The ability to colonize freshwater habitats is attributed to the fact that some species are euryhaline (Karsten and West 1993). Although there are few records of *Caloglossa* species with environmental data from strictly freshwater habitats, they have been reported in the following conditions: water temperature 23–24 °C, pH 7.6–8.4, conductivity 100–210  $\mu\text{S cm}^{-1}$ , current velocity 33–43  $\text{cm s}^{-1}$  (Sheath et al. 1993b).

**Distribution:** *Caloglossa* species have been reported in freshwater for several regions of the world including Africa, Asia, Australasia, North and South America, Pacific Islands, rarely from Europe (Sheath et al. 1993b; Kamiya and West 2014; Kamiya et al. 1999, 2003, 2016, 2017; Krayesky et al. 2011, 2012; West et al. 2008, 2015) (Fig. 3.7). The only primarily freshwater species seems to be *C. beccarii*, but it has also been reported from brackish water (Kamiya et al. 2016).

Key to the species of *Caloglossa* occurring in freshwater

1a	Branching of the main axis adventitious	2
1b	Branching of the main axis endogenous	4
2a	Wing cells consisting of 15–23 cell rows at the internode	<i>C. beccarii</i>
2b	Wing cells consisting of 2–12 cells rows at the internode	3
3a	Blades lanceolate, strongly constricted at the nodes	<i>C. fluviatilis</i>
3b	Blades strap-like, slightly constricted at the nodes	<i>C. ogasawaraensis</i>
4a	Rhizoids arising from axial and central periaxial cells	<i>C. leprieurii</i>
4b	Rhizoids arising from wing cells	5
5a	Blades strap-like, strongly constricted at the nodes	<i>C. vieillardii</i>
5b	Blades elliptical or lanceolate, slightly constricted at the nodes	<i>C. continua</i>



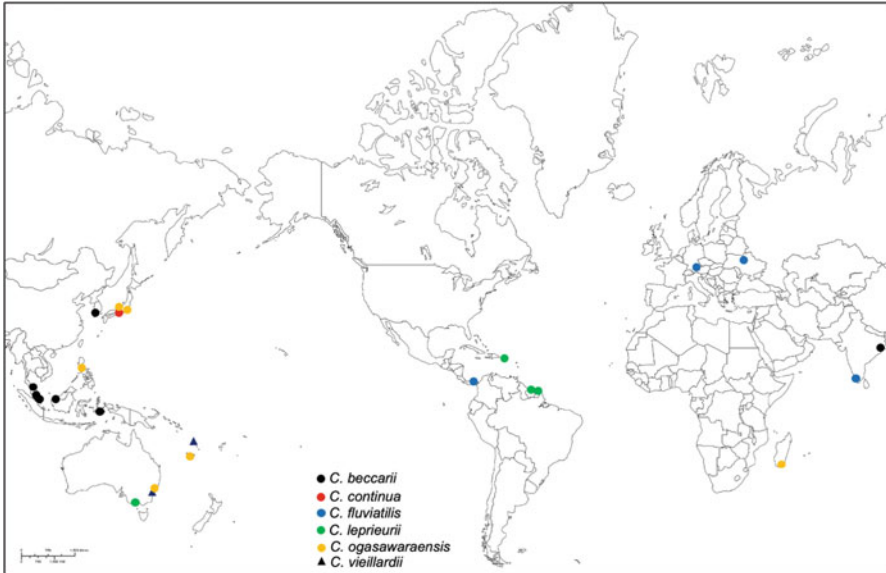


Fig. 3.7 World map showing the distribution of species of *Caloglossa* occurring in freshwater

*Caloglossa beccarii* (Zanardini) De Toni, Sylloge algarum, vol. 4:730 (1900)  
(Fig. 3.8a–c)

**Basionym:** *Delesseria beccarii* Zanardini, Mem Reale Ist Veneto Sci, Lettere ed. Arti 17:140 (1872).

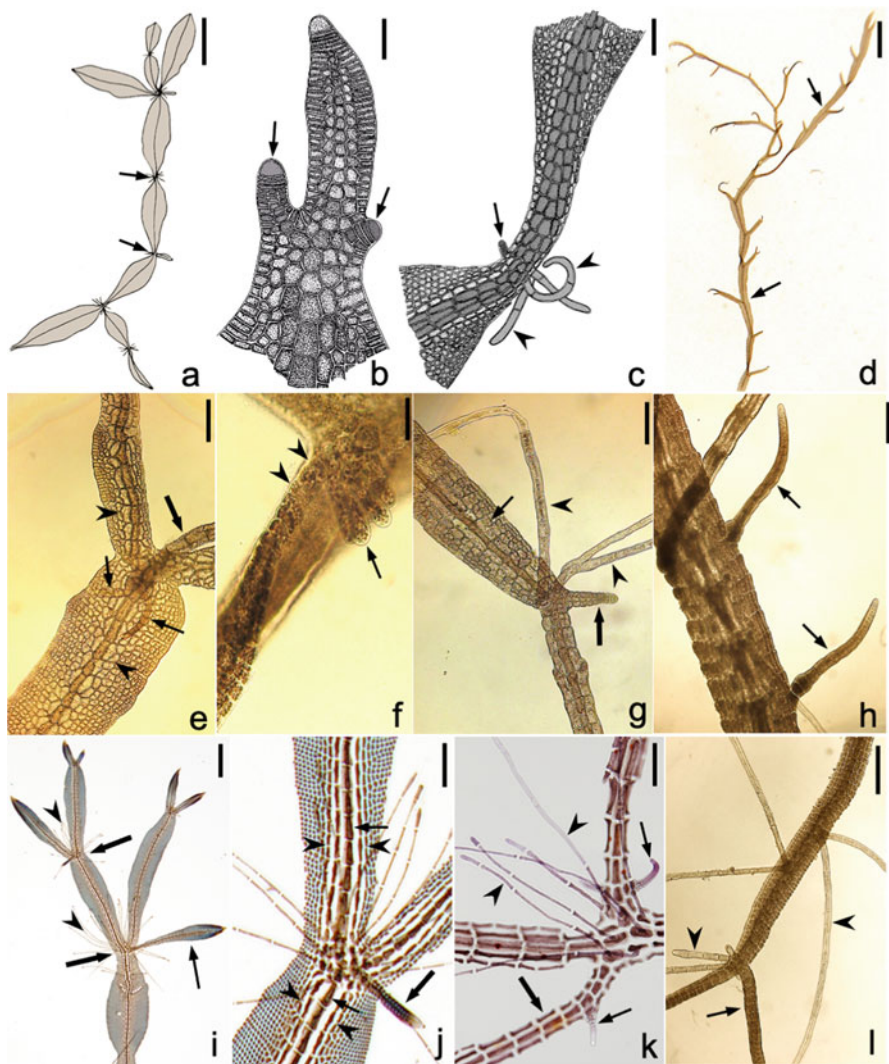
**Type:** L4045165, O Beccari (Lectotype, designated by King and Puttock 1994); L4045166 (Isolectotype).

**Type locality:** Malaysia, western Sarawak, near Gunung Pueh, 1.800° S, 109.683333° E (estimated).

**Description:** thalli dichotomously or less often trichotomously branched, attached by rhizoids that arise from pericentral cells at the nodes; mature blades elliptical, strongly to moderately constricted at the nodes; adventitious branches formed from lateral pericentral initials; endogenous branches absent; midrib consisting of an axial cell and four periaxial cells; wing cells consisting of 15–23 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: presence of adventitious branching and wing cells with 15–23 cell rows at the internode.

**Representative sequences in GenBank:** LC115027, LC115028 (*rbcL*).



**Fig. 3.8** (a–c) *Caloglossa beccarii*: (a) general view of thallus with constricted nodes (arrows); (b) apex with two adventitious branches (arrows); (c) nodal region with adventitious branch (arrow) and rhizoids (arrowheads); (d–f) *Caloglossa continua*: (d) general view of thallus with slightly constricted blades (arrows); (e) nodal region with young branch (large arrow), rhizoids (arrows) and midrib with two rows of periaxial cell per axial cell (arrowheads); (f) rhizoids developing from the marginal wing cells (arrow); (g, h) *Caloglossa fluviatilis*: (g) nodal region with a young adventitious branch (large arrow), midrib with two periaxial cell and one axial cell (arrow) and rhizoids (arrowheads); (h) young blade with adventitious branches (arrows); (i, j) *Caloglossa leprieurii*: (i) blades with slightly constricted nodes (large arrows), an endogenous branch (arrow) and rhizoids (arrowheads); (j) nodal region with an endogenous young branch (large arrow) and midrib with two periaxial cells (arrowheads) and a large axial cell (arrows); (k) *Caloglossa ogasawaraensis*: (k) nodal region with a large adventitious branch (large arrow), young adventitious branches (arrows) and rhizoids (arrowheads); (l) *Caloglossa vieillardii*: (l) nodal region with a young endogenous branch (arrow) and rhizoids (arrowheads). Scale bars: (a) = 2.5 mm; (d) = 1 mm; (i) = 500 µm; (c, j–l) = 100 µm; (b, d, e, g, h) = 50 µm; (f) = 25 µm (Image authors: Fig. (d–h, l) J West; (i–k) M Kamiya; Fig. (a–c) modified from Kumano (1979))



**Distribution:** Asia: India, Indonesia, Malaysia, Singapore, Thailand, Vietnam (Fig. 3.7).

**Key reference:** Kamiya et al. (2016).

**Remarks:** Kamiya et al. (2016) delineated *C. beccarii* based on molecular data and showed that some previous records in freshwater from India (West et al. 2015) represent *C. fluviatilis*.

*Caloglossa continua* (Okamura) King and Puttock, Austr Syst Bot 7:115 (1994) (Fig. 3.8d–f)

**Basionym:** *Caloglossa leprieurii* var. *continua* Okamura, Bot Mag Tokyo 17: 129 (1903).

**Type:** TI, K Okamura 67, vii.1902 (Lectotype, designated by King and Puttock 1994, not found); L4045173 (Isolectotype).

**Type locality:** Japan, Mikawa, Ishikawa Prefecture, river mouth of Ko-yahagi-gawa, 34.867841° N, 136.920425° E (estimated).

**Description:** thalli sub-dichotomously branched, attached by rhizoids that arise from marginal wing cells at the nodes; mature blades elliptical or lanceolate, slightly constricted at the nodes; adventitious branches absent; endogenous branches produced by an axial cell above the nodes; midrib consisting of an axial cell and four periaxial cells; wing cells consisting of 3–9 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: mature blades elliptical or lanceolate, slightly constricted at the nodes, presence of endogenous branching and rhizoids arising from wing cells.

**Representative sequences in GenBank:** AB023379, D89950 (*rbcL*).

**Distribution:** Asia: Japan (Fig. 3.7).

**Key reference:** Kamiya et al. (1999).

**Remarks:** the species concept proposed by Kamiya et al. (1999) is followed; this concept is based on molecular and morphological data with species distribution confirmed only from Japan.

*Caloglossa fluviatilis* Krayesky, Fredericq, and JN Norris, Phycologia 51:523 (2012) (Fig. 3.8g, h)

**Type:** US 01067291, Algae Type Collection 217746, BS Wysor, 421, 5.v.1999 (Holotype); US 01067293, LAF (Isotypes).

**Type locality:** Republic of Panama, Pedro Miguel, Pedro Miguel Lock, 8.996228° N, 79.591803° W.

**Description:** thalli sub-dichotomously branched, attached by rhizoids that arise from pericentral and marginal wing cells at the nodes; mature blades lanceolate, strongly constricted at the nodes; adventitious branches from lateral pericentral initials; endogenous branches absent; midrib consisting of an axial cell and four periaxial cells; wing cells consisting of 2–12 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: mature blades lanceolate, strongly constricted at the nodes, presence of adventitious branching and wing cells with 2–12 cell rows at the internode.

**Representative sequences in GenBank:** JN845515 (*rbcL*).

**Distribution:** Asia: India; Europe: Germany, Ukraine; North America: Republic of Panama (Fig. 3.7).

**Key references:** Kravesky et al. (2012), West et al. (2015), Kamiya et al. (2016).

**Remarks:** Kamiya et al. (2016) determined based on molecular data that previous records of *C. beccarii* from India (West et al. 2015) represent *C. fluviatilis*. In addition, two samples from Europe (Germany and Ukraine) should be assigned to this species, thus expanding its distribution more widely than the type locality in Panama. However, the genetic distance among the sequence from Panama with the others is very high (4.8–6.9% for *rbcL*) indicating they are most probably different species. Therefore, further investigation of *C. fluviatilis* is required to evaluate possible cryptic speciation.

*Caloglossa leprieurii* (Montagne) Martens, Flora 52:234, 237 (1869) (Fig. 3.8i, j)

**Basionym:** *Delesseria leprieurii* Montagne, Ann Sci Nat, Bot 13:196 (1840).

**Type:** PC, FR Leprieur 356, 362 (Lectotype, designated by King and Puttock 1994, not found); L 4045224, 4045226 (Isolectotypes).

**Type locality:** French Guiana, near Cayenne, 4.903348° N, 52.358251° W (estimated).

**Description:** thalli sub-dichotomously branched, attached by rhizoids from axial and central periaxial cells at the nodes; mature blades elongate-elliptical or lanceolate, slightly to strongly constricted at the nodes; adventitious branches absent; endogenous branches produced by an axial cell above the nodes; midrib consisting of an axial cell and four periaxial cells; wing cells consisting of 8–38 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: mature blades lanceolate or elongate-elliptical, strongly constricted at the nodes, presence of endogenous branching and rhizoids arising from axial and central periaxial cells.

**Remarks:** the species concept proposed by Kravesky et al. (2011) based on combined molecular and morphological excludes other species previously assigned to the *C. leprieurii* complex (*C. apomeiotica* and *C. apicula*) and a new species (*C. ruetzleri*).

**Representative sequences in GenBank:** HM775463, HM775465, HM775467 (*rbcL*).

**Distribution:** North America: Puerto Rico; South America: French Guiana, Guyana, Suriname (Fig. 3.6).

**Key references:** Sheath et al. (1993b), Kravesky et al. (2011).

*Caloglossa ogasawaraensis* Okamura, Bot Mag Tokyo 11:13 (1897) (Fig. 3.8k)

**Type:** PC, FR Leprieur, 20.xi.1841 (Holotype, not found); L 4045224, 4045226 (Isotypes).

**Type locality:** French Guiana, Sinnamary, 5.374671° N, 52.954603° W (estimated).

**Description:** thalli dichotomously or less often trichotomously branched, attached by rhizoids from pericentral cells at the nodes; mature blades strap-like or lanceolate, slightly constricted at the nodes; adventitious branches formed from lateral pericentral initials; endogenous branches absent; midrib consisting of an axial cell and four periaxial cells; wing cells consisting of 2–8 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: mature blades strap-like or lanceolate, slightly constricted at the nodes, presence of adventitious branching and wing cells with 2–8 cell rows at the internode.

**Representative sequences in GenBank:** AB862544, AB862545, AB862551 (*rbcL*).

**Distribution:** Africa: Madagascar; Asia: Japan, Philippines; Australasia: Australia, New Caledonia (Fig. 3.7).

**Key references:** Sheath et al. (1993b), Kamiya and West (2014).

**Remarks:** molecular analyses based on three markers by Kamiya and West (2014) suggested that this species is divided into three groups: Australian, Melanesian, and Micronesian specimens; western Pacific coasts, Micronesia, and Madagascar specimens; and eastern Pacific-Atlantic and Malaysian specimens. Although the genetic variation suggests speciation of the three phylogenetic groups, taxonomically informative morphological characters are required to describe them as distinct species.

*Caloglossa vieillardii* (Kützing) Setchell, Publ Carnegie Inst Washington 341:161 (1924) (Fig. 3.8l, 3.9a)

**Basionym:** *Hypoglossum vieillardii* Kützing, Diagnosen und Bemerkungen zu drei und siebenzig neun Algen species:19 (1863).

**Type:** L4045254, E Vieillard, i.1863 (Lectotype), L4045255 (Isolectotype).

**Type locality:** New Caledonia, Wagap, 20.833333° S, 165.266667° E (estimated).

**Description:** thalli dichotomously branched, attached by rhizoids that arise from pericentral cells at the nodes; mature blades strap-like or elongate-elliptical, strongly constricted at the nodes; adventitious branches absent; endogenous branches produced by an axial cell above the nodes; midrib consisting of an axial cell and two periaxial cells; wing cells consisting of 2–8 second- and third-order cell rows at the internode.

**Diagnostic characters:** this species can be differentiated from other species of *Caloglossa* occurring in freshwater by the following combination of characters: mature blades strap-like or elongate-elliptical, strongly constricted at the nodes, presence of endogenous branching and rhizoids arising from pericentral cells.

**Representative sequences in GenBank:** LC321956 (*rbcL*).

**Distribution:** Australasia: Australia; Pacific Islands: Vanuatu (Fig. 3.7).

**Key references:** Kamiya et al. (2003, 2017), West et al. (2008).

**Dubious records of *Caloglossa* in freshwater:** A record of *C. saigonensis* Tanaka and Pham-Hoang by Kumano (2002) was based on the description by Jao (1941, as *C. leprieurii* var. *angusta* Jao) from China, which is currently treated as a synonym of *C. saigonensis*. However, there are no molecular data to confirm if it represents this species according to the current species concept based on molecular and morphological evidence. Thus, this species should not be considered as occurring in freshwater until further studies.

**Family Rhodomelaceae** Horaninow, *Characteres essentialia familiarum ac tribuum regni vegetabilis*:238 (1847)

The characteristics of the family can be summarized as follows (adapted from Huisman 2017): thalli usually erect, abundantly branched, in some genera foliose and/or prostrate, branches cylindrical, compressed or flat; all erect branches similar or with indeterminate branches bearing determinate laterals of limited growth; adventitious branching in some genera; basal attachment by holdfast discoid or fibrous or by rhizoids; growth monopodial by transverse or oblique divisions of apical cells; transverse divisions followed by longitudinal divisions to form pericentral cells and the oblique divisions giving rise to laterals; pericentral cells 4–24, cut-off in alternating order, ecorticate or corticate; cortex parenchymatous or rhizoidal or with rhizoids separating the pericentral or cortical cell; cells uni- or multinucleate; plastids usually discoid.

***Bostrychia*** Montagne, *Histoire de l’Ile de Cuba, Botanique, Plantes Cellulaires*:39 (1842b)

**Type species:** *Bostrychia scorpioides* (Hudson) Montagne, *Dictionnaire Universel d’Histoire Naturelle*:661 (1842a).

**Description:** Thalli dark reddish, dichotomously, pseudodichotomously or alternately branched, axes corticated or ecorticate, attached to substrate by haptera (specialized rhizoidal branches), arising terminally on special branches (“cladohaptera”) or arising laterally on peripheral cells (“peripherohaptera”); main axes determinate, polysiphonous consisting of axial cells with 2–6 whorls of 4–9 pericentral cells; determinate axes formed laterally to main axes with monosiphonous or polysiphonous ultimate branches; reproductive structures typically observed in freshwater populations, tetrasporangia consisting of inflated, multichambered structures, termed stichidia, on the upper portion of the lateral branches; tetrasporangia tetrahedrally divided, whorled; stichidia on determinate laterals, up to 25 segments in length, fertile segments with 4–5 pericentral cells and tetrasporangia, each protected by 2–3 cover cells, often subdivided. Carpogonia and cystocarps described for only one species in freshwater.

**Habitat:** freshwater populations may be found in strictly freshwater habitats, but generally occur in brackish water areas, such as river estuaries and mangroves and in some localities, they can colonize upstream segments with no saltwater influence. The ability to colonize freshwater habitats is attributed to the fact that populations of some species are euryhaline (Karsten et al. 1994). *Bostrychia* species have been reported in the following conditions: water temperature 17–26 °C, pH 7.0–8.4, conductivity (38–)70–840  $\mu\text{S cm}^{-1}$ , current velocity 0–66  $\text{cm s}^{-1}$  (Sheath et al. 1993b; Necchi et al. 1999).

**Distribution:** species of *Bostrychia* have been reported in tropical and sub-tropical, less often, in temperate regions of Australasia, Asia, North and South America (Fig. 3.10). Some species have been reported to have a broad geographic distribution (e.g., *B. moritziana* and *B. radicans*), while others are more geographically restricted (e.g., *B. kelanensis*, *B. scorpioides*, and *B. tenella*), but there is no distinct geographic trend for a particular species to be found in freshwater for specific regions.

**Remarks:** there are some reports of *Bostrychia* species in brackish waters, such as mangroves or river estuaries (e.g., Ganesan et al. 2018 from India); these records were not included and only published records showing that the localities represent habitats without the direct influence of salt water are listed.

Key to the species of *Bostrychia* occurring in freshwater

1a	Attachment by rhizoidal cells arising from the proliferation of peripheral and axial cells terminating a specialized branch (cladohapteron)	2
1b	Attachment by rhizoidal cells arising from proliferation of peripheral cells on the indeterminate axis (peripherohapteron)	4
2a	Apices of determinate branches monosiphonous	<i>B. moritziana</i>
2b	Apices of determinate branches polysiphonous	3
3a	Two whorls of pericentral cells (tier cells) per axial cell	<i>B. radicans</i>
3b	Three whorls of pericentral cells (tier cells) per axial cell	<i>B. kelanensis</i>
4a	Main axes corticate	5
4b	Main axes ecorticate	6
5a	Apices of determinate branches curled	<i>B. scorpioides</i>
5b	Apices of determinate branches straight	<i>B. tenella</i>
6a	Branching alternate	<i>B. flagellifera</i>
6b	Branching pseudodichotomous or dichotomous	<i>B. hamana-tokidae</i>

*Bostrychia flagellifera* Post, Rev Algal 9:34 (1936) (Fig. 3.9b–d)

**Basionym:** *Bostrychia tenella* subsp. *flagellifera* (Post) King and Puttock, Phycologia 27:18 (1988).

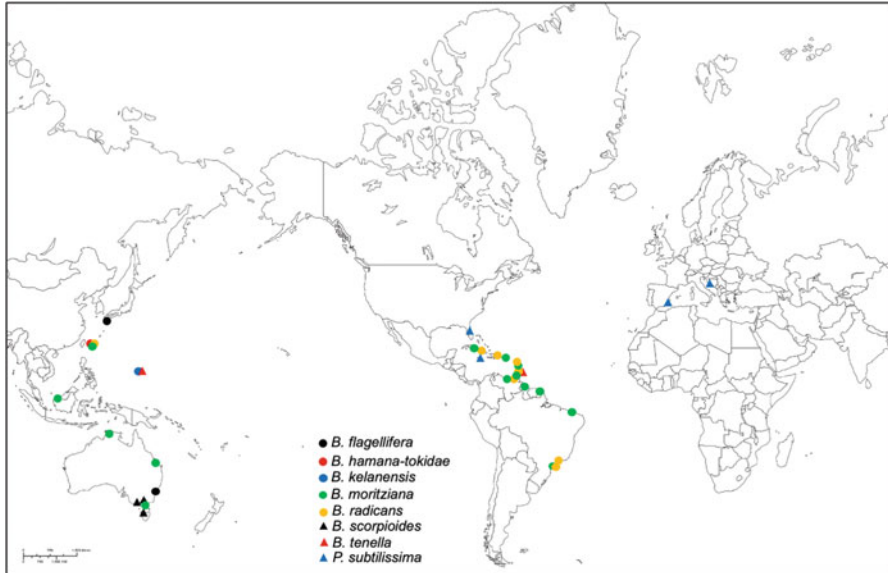
**Type:** MEL 672239A, 1847 (Lectotype, designated by King and Puttock 1989).

**Type locality:** Australia, New South Wales, Sydney, Paramatta River, 33.81670° S, 151.01670° E (estimated).



**Fig. 3.9** (a) *Caloglossa vieillardii*: (a) nodal region with endogenous branches (large arrows) and midrib with one row of periaxial cells (arrowheads) per axial cell (arrows) (b–d) *Bostrychia flagellifera*: (b) general view of thallus with alternate primary (arrows) and secondary (arrowheads) branches; (c) main axis with alternate primary (large arrows) and secondary (arrows) branches and monosiphonous determinate branches (arrowheads); (d) determinate lateral branch with tetrasporangial stichidium (large arrow) and monosiphonous determinate branch (arrow); (e–g) *Bostrychia hamana-tokidai*: (e) main axis with dichotomous primary (large arrow) and secondary (arrow) branch and monosiphonous determinate branches (arrowhead); (f) peripherohapteron; (g) apex with dichotomous branches (arrows); (h–j) *Bostrychia kelanensis*: (h) general view of thallus with a basal disc (large arrow) and dichotomous branches (arrows); (i) main axis with three whorls of periaxial cells (arrowheads) and one axial cell (arrow); (j) cladohapteron; (k–n) *Bostrychia moritziana*: (k) main axis with dichotomous branches (large arrows) and tetrasporangial stichidia (arrowheads); (l) tetrasporangial stichidia (large arrows) and monosiphonous tips (arrows); (m) main axis with periaxial cells; (n) apex with a cladohapteron (arrow) and monosiphonous determinate branches (arrowheads); (o) *Bostrychia radicans*: apex with polysiphonous determinate branches (arrows). Scale bars: (h, k) = 1 mm; (b) = 500 µm; (o) = 200 µm; (c–e, l, n) = 100 µm; (a, f, g, i, m) = 50 µm; (j) = 25 µm (Image authors: Fig. (a–e, g–i, k–m, o) J West; Fig. (f, j) modified from Kumano (1979); Fig. (n) modified from Kumano and Necchi (1987))





**Fig. 3.10** World map showing the distribution of species of *Bostrychia* and *Polysiphonia* occurring in freshwater

**Description:** thalli alternately branched, main axes ecorticate, attached to the substrate by peripherohaptera; apices of determinate branches monosiphonous, straight; axial cells with two whorls of pericentral cells; tetrasporangial stichidia slender, elongate-ellipsoidal or fusiform, terminal portion polysiphonous; each tetrasporangium with one supporting cell and two cover cells.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis ecorticate, alternately branched and rhizoidal cells arising from peripheral cells on the indeterminate axis (peripherohapteron).

**Representative sequences in GenBank:** AY920854, AY920856, AY920856 (LSU rDNA).

**Distribution:** Asia: Japan; Australasia: Australia (Fig. 3.10).

**Key references:** King and Puttock (1989), Zuccarello and West (2006).

**Remarks:** Zuccarello and West (2006) showed that *B. tenella* subsp. *flagellifera* is genetically distinct from *B. tenella* and that the morphological distinction between them (branching frequency) is consistent. They reinstated the species level status as originally conceived by Post (1936).

*Bostrychia hamana-tokidai* Post, Beih Bot Centralb 61:208 (1941) (Fig. 3.9e–g)

**Type:** Hamana, xi.1938 (Holotype, not found).

**Type locality:** Japan, Kyushu, Kagoshima Prefecture, Makurazaki, Kedo River, 31.272866° N, 130.296692° E (estimated).



**Description:** thalli dichotomous, trichotomous or pseudodichotomously branched, main axes ecorticate, attached to the substrate by peripherohaptera; apices of determinate branches monosiphonous, straight; axial cells with two whorls of pericentral cells; reproductive structures not observed in freshwater populations.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis ecorticate, with pseudodichotomous or dichotomous branching and rhizoidal cells arising from peripheral cells on the indeterminate axis (peripherohapteron).

**Representative sequences in GenBank:** MF782659 (*rbcL*).

**Distribution:** Asia: Japan (Fig. 3.10).

**Key references:** Post (1941), Kumano (1979), Zuccarello et al. (2018).

**Remarks:** this species was regarded as a synonym of *B. simpliciuscula* Harvey ex J Agardh (King and Puttock 1989), but it was recently reinstated based on DNA sequence data (Zuccarello et al. 2018). It represents a lineage with the morphology of *B. simpliciuscula* but only occurs on the main islands of Japan. A report of this species by Kumano (1979) from Iriomote Island, Okinawa, which is not part of the main islands is provisionally assigned to *B. hamana-tokidae* until further confirmation by DNA sequence data.

*Bostrychia kelanensis* Grunow *ex* Post, Rev Algolog 9:20 (1936) (Fig. 3.9h–j)

**Type:** L Kärnbach 40, viii.1888 (Holotype, not found).

**Type locality:** Asia: Papua New Guinea, Kelanoa, 6.006842° S, 147.497075° E (estimated).

**Description:** thalli dichotomous or pseudodichotomously branched, main axes ecorticate, attached to the substrate by cladohaptera; apices of determinate branches polysiphonous, straight; axial cells with three whorls of pericentral cells; tetrasporangial stichidia slender, fusiform or ellipsoidal, terminal portion polysiphonous; each tetrasporangium with one supporting cell and three cover cells.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis ecorticate, apices of determinate branches polysiphonous and straight, three whorls of pericentral cells per axial cell and rhizoidal cells arising from the proliferation of peripheral and axial cells terminating a specialized branch (cladohapteron).

**Representative sequences in GenBank:** AY920853, KC768876 (*rbcL*).

**Distribution:** Pacific Islands: Guam (Fig. 3.10).

**Key references:** King and Puttock (1989), Zuccarello and West (2006).

**Remarks:** Zuccarello and West (2006) in a molecular phylogenetic study showed that *Stictosiphonia kelanensis* grouped with *Bostrychia* species with cladohaptera although in an ambiguous position and proposed that all species of *Stictosiphonia* to be *Bostrychia*.

***Bostrychia moritziana*** (Sonder ex Kützing) J Agardh, Species genera et ordines algarum:862–863 (1863) (Fig. 3.9k–n)

**Basionym:** *Polysiphonia moritziana* Sonder ex Kützing Species algarum:838 (1849).

**Type:** MEL 672271A, K Moritz 142 (Lectotype, designated by Womersley 2003: 366).

**Type locality:** Venezuela, Cumaná, 10.431916° N, 64.183316° W (estimated).

**Description:** thalli dichotomous or pseudodichotomously branched, main axes ecorticate, attached to the substrate by cladophaptera; apices of determinate branches monosiphonous, straight; axial cells with two whorls of pericentral cells; tetrasporangial stichidia slender, elongate-ellipsoidal or fusiform, terminal portion monosiphonous; each tetrasporangium with one supporting cell and two cover cells.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis ecorticate, apices of determinate branches monosiphonous and straight and rhizoidal cells arising from the proliferation of peripheral and axial cells terminating a specialized branch (cladophapteron).

**Representative sequences in GenBank:** MF093965 (COI-5P); AF126703, AY260875, AY920814 (*rbcL*).

**Distribution:** Asia: Japan; Australasia: Australia; North America: Cuba, Dominica, Grenada, Guadeloupe, Martinique, Puerto Rico, Saint Lucia, Trinidad and Tobago; South America: Brazil, French Guiana, Guyana, Venezuela (Fig. 3.9).

**Key references:** Kumano (1979), D’Lacoste and Ganesan (1987), Sheath et al. (1993b), Zuccarello and West (2003).

**Remarks:** this species is the most widely reported in freshwater, being recorded for several continents (Fig. 3.9). The report of carpogonia and cystocarps, as well as stichidia from Venezuela by D’Lacoste and Ganesan (1987) is the only record of gametangia in a freshwater population.

***Bostrychia radicans*** (Montagne) Montagne, Dictionnaire Universel d’Histoire Naturelle:661 (1842a) Fig. 3.9o)

**Basionym:** *Rhodomela radicans* Montagne, Ann Sci Nat, Bot, Seconde Série 13: 198 (1840).

**Type:** MEL 672285A, FMR Leprieur 361 (Lectotype, designated by King and Puttock 1989); PC0046492 (Isolectotype).

**Type locality:** French Guiana, near Cayenne, 04.922420° N, 52.313453° W (estimated).

**Description:** thalli dichotomous or pseudodichotomously branched, main axes ecorticate, attached to the substrate by cladophaptera; apices of determinate branches polysiphonous, straight; axial cells with two whorls of pericentral cells; tetrasporangial stichidia ellipsoidal, terminal portion polysiphonous; each tetrasporangium with one supporting cell and two cover cells.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis ecorticate, apices of determinate branches polysiphonous and straight, two whorls of pericentral cells per axial cell and rhizoidal cells arising from the proliferation of peripheral and axial cells terminating a specialized branch (cladophapteron).

**Representative sequences in GenBank:** AY920818, AY920821, AY920822 (*rbcL*).

**Distribution:** Asia: Japan; North America: Cuba, Dominique, Dominican Republic, Grenada, Guadeloupe; South America: Brazil, Venezuela (Fig. 3.10).

**Key references:** Kumano (1979), Sheath et al. (1993b), Zuccarello and West (2003, 2006).

**Remarks:** this species is often reported in freshwater, being recorded on several continents (Fig. 3.9) and the genetic diversity suggests potential cryptic species across its geographic distribution (Zuccarello and West 2003).

*Bostrychia scorpioides* (Hudson) Montagne, Dictionnaire Universel d'Histoire Naturelle:661 (1842a) (Fig. 3.11a, b)

**Basionym:** *Fucus scorpioides* Hudson, Flora Anglica: 471 (1762).

**Type:** OXF, Dillenius's herbarium (Holotype, not found).

**Type locality:** England, West Sussex, 50.928033° N, 0.461733° W (estimated).

**Description:** thalli dichotomous or pseudodichotomously branched, main axes corticated, attached to the substrate by peripherohaptera; apices of determinate branches polysiphonous, curled; axial cells with one whorl of pericentral cells; reproductive structures not observed in freshwater populations.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis corticated, apices of determinate branches polysiphonous and curled and rhizoidal cells arising from peripheral cells on the indeterminate axis (peripherohapteron).

**Representative sequences in GenBank:** MF094019 (COI-5P); AY920825 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 3.10).

**Key references:** Entwisle and Kraft (1984), King and Puttock (1989), Zuccarello and West (2006).

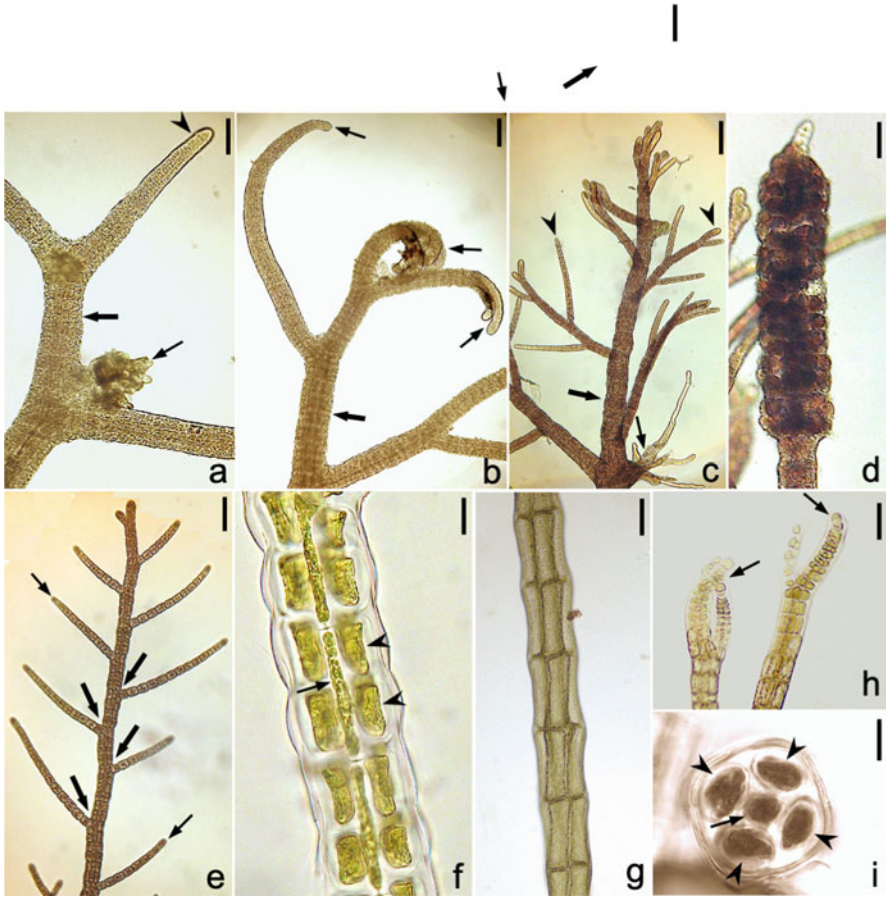
*Bostrychia tenella* (JV Lamouroux) J Agardh, Species genera et ordines algarum:869 (1863) (Fig. 3.11c-f)

**Basionym:** *Plocamium tenellum* JV Lamouroux, Ann Mus Hist Nat 20:138 (1813).

**Type:** MEL 672309A, H West (Syntypes).

**Type locality:** United States Virgin Island, Saint Croix, 17.72887° N, 64.759702° W (estimated).

**Description:** thalli alternately branched, main axes corticated, attached to the substrate by peripherohaptera; apices of determinate branches monosiphonous, straight; axial cells with two whorls of pericentral cells; tetrasporangial stichidia



**Fig. 3.11** (a, b) *Bostrychia scorpioides*: (a) main corticated axis (large arrow) with a peripherohapteron (arrow) and polysiphonous determinate branches (arrowhead); (b) main corticated axis (large arrow) with curled apices of determinate branches (arrows) (c–f) *Bostrychia tenella*: (c) main corticated axis (large arrow) and monosiphonous determinate branches (arrows); (d) tetrasporangial stichidium; (e) apex with alternate branches (large arrows) and monosiphonous determinate branches (arrows); (f) main axis with two whorls of periaxial cells (arrowheads) and one axial cell (arrow); (g–i) *Polysiphonia subtilissima*: (g) main axis with periaxial cells; (h) apices with polysiphonous determinate branches (arrows); (i) cross section of main axis with one axial cell (arrow) and four periaxial cells (arrowheads). Scale bars: (c) = 250  $\mu\text{m}$ ; (a, b) = 200  $\mu\text{m}$ ; (g) = 100  $\mu\text{m}$ ; (d–f, h) = 50  $\mu\text{m}$ ; (i) = 25  $\mu\text{m}$  (Image authors: Fig. (a–f) J West)

cylindrical or ellipsoidal, terminal portion polysiphonous; each tetrasporangium with one supporting cell and two cover cells.

**Diagnostic characters:** this species can be differentiated from other species of *Bostrychia* occurring in freshwater by the following combination of characters: main axis corticated, apices of determinate branches monosiphonous and straight and rhizoidal cells arising from peripheral cells on the indeterminate axis (peripherohapteron).

**Representative sequences in GenBank:** KP796017, KP796020, KP796024 (*rbcL*).

**Distribution:** North America: Barbados; Pacific Islands: Guam (Fig. 3.10).

**Key references:** Kumano (1979), Sheath et al. (1993b), Zuccarello et al. (2018).

**Remarks:** this species has been treated as morphologically variable and several species were included as synonyms (King and Puttock 1989). Zuccarello et al. (2015) showed five genetic species in the *B. tenella* complex but recognized only three morphological entities: one clade representing *B. binderi* which was resurrected, a second was recognized as *B. montagnei* based on morphology and a third lineage consisted of two genetic lineages within the new circumscription of *B. tenella*, with long monosiphonous determinate laterals, and having a wide geographic distribution.

*Polysiphonia* Greville, Scottish cryptogamic flora:90 (1824a)

**Type species:** *Polysiphonia stricta* (Mertens ex Dillwyn) Greville, Flora edinensis:309 (1824b).

**Description:** thalli forming tufts, erect or prostrate, irregularly branched; uniaxial with four to many pericentral cells; trichoblasts and branches at apices, generally 1 per segment in a spiral pattern; scar cells evident from shed trichoblasts; secondary cortication present in some species; carpogonia and carposporangia arranged in cystocarps formed laterally on polysiphonous branches, ovoidal or spherical, ostiolate; spermatangia in heads, on fertile trichoblasts or replacing them; tetrasporangia tetrahedral, spherical, in a series in polysiphonous branches. No reproductive structures observed in freshwater populations.

**Remarks:** this genus is primarily marine and only *P. subtilissima* has been reported from freshwaters.

*Polysiphonia subtilissima* Montagne, Annales des Sciences Naturelles, Botanique, Seconde Série 13:199 (1840) (Fig. 3.11g–i)

**Type:** PC, Herb. Montagne, Leprieur 682 (Holotype); BM000530488, BM000937021, BM000937025 (Isotypes).

**Type locality:** French Guiana, Cayenne, 4.944627° N, 52.320380° W (estimated).

**Description:** thalli blue or reddish-brown in color, (2.1–)11.6–44.2 mm in length, (36.1–)50.5–109 µm in diameter, pericentral cells 4–5, 56.3–156 µm in length, (8.3–)16.6–30.6 µm in diameter; trichoblasts abundant or scarce.

**Diagnostic characters:** this is the only species recorded from freshwaters.

**Representative sequences in GenBank:** JX294915 (COI-5P), JX294917, MN418387 (*rbcL*).

**Habitat:** although this species has been reported only infrequently in freshwaters, there are physical and chemical parameters for most reports. In North America, it has been reported from rivers with pH 7.7–7.8, water temperature 22–26 °C, and conductivity 1150–1840 µS cm<sup>-1</sup> (Sheath et al. 1993a, b). In Europe, this species has been recorded from rivers and lake habitats in Spain (pH 7.6–8.8, conductivity 1900–2700 µS cm<sup>-1</sup>) and Croatia (pH 7.6, water temperature 20 °C, conductivity 770 µS cm<sup>-1</sup>) (Lam et al. 2013; Koletić et al. 2020a, b). These

European freshwater reports were close to brackish locations, from which this species has also been recorded.

**Distribution:** Europe: Croatia, Spain; North America: Jamaica, the USA (Fig. 3.10).

**Key references:** Sheath et al. (1993b), Lam et al. (2013), Koletić et al. (2020a, b).

**Remarks:** the description provided is based on the freshwater records and type specimen only; the freshwater populations have been reported to be smaller than the marine populations. There is a record from the Hudson River in West Point New York by Harvey (1853), but it is uncertain if the location is strictly freshwater or brackish.

**Order Gigartinales** F Schmitz, Syllabus der Vorlesungen über specielle und medicinisch-pharmaceutische Botanik:18 (1892)

Members of Gigartinales are characterized by (adapted from Lindstrom 2017): thalli uncalcified, erect or crustose, terete, flattened or foliose, branched or unbranched, sometimes proliferous; alternation of isomorphic or heteromorphic generations, with heteromorphic members having macroscopic gametophyte; monoecious or dioecious; procarpic or non-procarpic; tetrasporangia cruciate or zonate; pit plugs without cap layers.

Gigartinales is a very diverse group encompassing 36 families and 170 genera (Lindstrom 2017), but scarcely represented in freshwater with only one genus (*Sterrocladia*). According to Sherwood et al. (2012), molecular phylogenetic analyses of one freshwater species (*Sterrocladia belizeana*) indicated unequivocally that it was member of the Gigartinales. However, this species was positioned basal to the Gigartinaceae and Phyllophoraceae clades, likely representing a novel family. Thus, the classification of *Sterrocladia* in the Caulacanthaceae is provisional until a more thorough phylogenetic analysis of the genus and related genera in the Gigartinales can be completed.

**Family Caulacanthaceae** Kützing, Phycologia generalis:393 (1843)

The characteristics of the family can be summarized as follows (adapted from Huisman 2017): thalli erect or entangled, branches terete or compressed; uniaxial or with small group of apical cells; axial cell with one or two periaxial cells producing a medulla of either lax periaxial filaments (without rhizoids) or sub-spherical cells, with the axial filament distinct throughout or soon inconspicuous and a cortex of sub-spherical cells; life history isomorphic.

***Sterrocladia*** F Schmitz, Flora 77:389 (1893)

**Type species:** *Sterrocladia amnica* (Montagne) F Schmitz, Flora 77:388 (1893).

**Description:** thalli pseudoparenchymatous, cylindrical, pseudodichotomously branched, with main axes and branches of similar size; apices rounded and mucronated with a prominent apical cell or acute; uniaxial construction in cross section, axial cell surrounded by one layer of large medullary cells and 1–3 layers of cortical cells; medulla compact and adherent or loosely aggregated and





**Fig. 3.12** World map showing the distribution of species of *Pneophyllum* and *Sterrocladia*

non-adherent to the outer cortex in cross section; axial cells, in one row, cylindrical to ellipsoidal in longitudinal section, surrounded by medullary and cortical cells; cortical cells small, irregularly shaped, polygonal and densely arranged in surface view; reproductive structures in nemathecia, forming wart-like protuberances on the thallus surface; nemathecia composed of short, branched filaments, producing terminal sporangia.

**Habitat:** the two species have been reported in montane streams of tropical rain forest areas with no environmental data available.

**Distribution:** the type species, *S. amnica*, from French Guiana and Guyana (South America) and *S. belizeana*, from Belize (North America), are rarely reported in these regions (Necchi 2016) (Fig. 3.12).

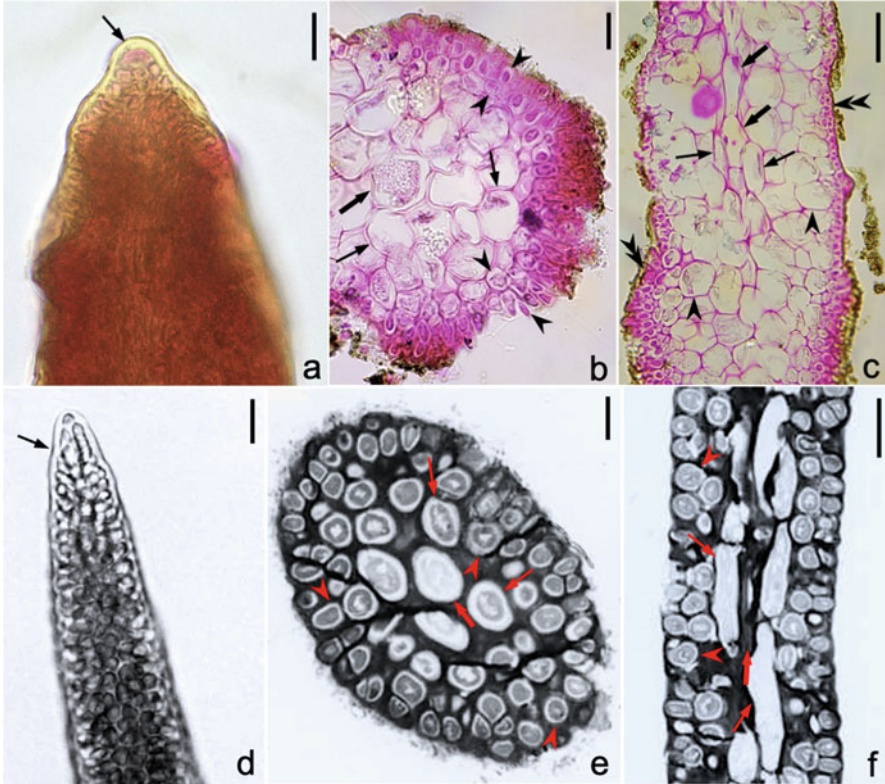
**Remarks:** it is uncertain if the structures referred to as sporangia are sporangia or spermatangia, but their large size (16–20  $\mu\text{m}$  in length, 15–19  $\mu\text{m}$  in diameter) and the presence of chloroplasts suggest sporangia. If sporangia, they could be asexual monosporangia, carposporangia, or young (undivided) tetrasporangia. Within *Sterrocladia* only two species, *S. amnica* and *S. belizeana*, have been described and are differentiated based on vegetative characters.

*Sterrocladia amnica* (Montagne) F Schmitz, Flora 77:388–389 (1893) (Fig. 3.13a–c)

**Basionym:** *Gymnogongrus amnicus* Montagne, Ann Sci Nat, Bot 14:289 (1850).

**Type:** PC 0058868, Montagne collection, FR Leprieur 1112 (Lectotype, designated by Sherwood et al. 2012); PC0602828, PC0602829, PC0602830 (Isolectotypes).





**Fig. 3.13** (a–c) *Sterrocladia amnica*: (a) apex mucronated with a prominent apical cell (arrow); (b) cross section with axial cells (large arrow), large (small arrows), and small cortical cells (arrowheads); (c) longitudinal section with axial cells (large arrow), medullary cells (small arrows), large (arrowheads) and small cortical cells (double arrowheads); (d–f) *Sterrocladia belizeana*: (d) apex acute attenuating towards the tip (arrow); (e) cross section with axial cells (large arrow), medullary cells (small arrows), and cortical cells (arrowheads); (f) longitudinal section with axial cells (large arrow), medullary cells (small arrows) and cortical cells (double arrowheads) Scale bars: (a–c, f) = 20  $\mu\text{m}$ ; (d, e) = 10  $\mu\text{m}$  (Fig. (c) reprinted with permission by Springer from Necchi (2016); Fig. (d–f) reprinted with permission by Taylor and Francis from Sherwood et al. (2012))

**Type locality:** French Guiana, Kaw, approximately 100 km from Cayenne and 40 km from the sea, 4.564288° N, 52.205935° W (estimated).

**Description:** thalli 150–215  $\mu\text{m}$  in diameter; apices rounded, slightly mucronated with a prominent apical cell; axial cells adherent to the outer cortex, surrounded by 2–3 inner layers of large, irregular medullary cells in cross section, 24–36  $\mu\text{m}$  in diameter; medulla compact, cells tightly arranged in cross section; axial cells one row, cylindrical to ellipsoidal in longitudinal section, 40–67  $\mu\text{m}$  in length, 13–22  $\mu\text{m}$  in diameter; cortical cells markedly different in size, inner layer large cells, outer layer small cells; inner cortical cells, two layers, rarely three, spherical

to ovoidal, 17–35 µm in diameter; outer cortical cells, 1 layer, rarely 2, small, irregularly shaped, polygonal, densely arranged, 6.0–11.5 µm in length, 4.5–8.5 µm in diameter; reproductive structures in nemathecium, forming wart-like protuberances on the thallus surface; nemathecium internal structure not clearly discernible in dried type specimens.

**Diagnostic characters:** this species is distinct from *S. belizeana* by the following vegetative characters: apices mucronated with a prominent apical cell, medulla compact with cells tightly aggregated, cortex forming two distinct layers (inner cells large and outer cells small).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** South America: French Guiana, Guyana (Fig. 3.12).

**Key references:** Skuja (1944), Sherwood et al. (2012).

*Sterrocladia belizeana* AR Sherwood, Necchi, AL Carlile, HD Laughinghouse and Sheath, Phycologia 51:632 (2012) (Fig. 3.13d–f)

**Type:** US 217873, HD Laughinghouse, 20.vii.2010 (Holotype); US 217874, BISH 751591, BISH 751592 (Isotypes).

**Type locality:** Belize, Stann Creek District, 16.16.8140° N, 88.3990° W.

**Description:** thalli 50–120 µm in diameter; apices acute, slightly attenuated towards the apex; axial cells not adherent to the outer cortex, surrounded by one layer of large medullary cells viewed in cross section, slightly larger than medullary cells, 8–17 µm in diameter; medulla loosely arranged, cells in filaments not tightly aggregated in cross section; axial cells, one row in longitudinal section, cylindrical to elongate-ellipsoidal, 20–40 µm in length, 7–14 µm in diameter; cortical cells, 2–3 layers of similar sized cells, small, sub-spherical to irregular in shape, loosely arranged, 6.0–7.5 µm in length, 3.0–5.0 µm in diameter; reproductive structures not observed.

**Diagnostic characters:** this species is distinct from *S. amnica* by the following vegetative characters: apices acute, slightly attenuated towards the apex, medulla loosely arranged with cells not tightly aggregated, cortex with no distinction between inner and outer layers in cell size.

**Representative sequences in GenBank:** JQ963344 (COI-5P); JQ963342 (*rbcL*).

**Distribution:** North America: Belize (Fig. 3.12).

**Key references:** Sherwood et al. (2012).

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# Chapter 4

## Subphylum Eurhodophytina, Class Florideophyceae, Subclass Nemaliophycidae, Orders Acrochaetiales, Balbianiales, and Thoreaales



Morgan L Vis and Orlando Necchi Jr

**Abstract** The orders Balbianiales and Thoreaales of the subclass Nemaliophycidae are composed of exclusively freshwater members, whereas the Acrochaetiales have marine or freshwater representatives, with the two families (Audouinellaceae and Ottiaceae) having exclusively freshwater representatives. Balbianiales has two genera (*Balbiana* and *Rhododraparnaldia*) each one with a single species. Audouinellaceae and Ottiaceae are monotypic with the genera *Audouinella* and *Ottia*, respectively. Five species are recognized within the genus *Audouinella*, whereas *Ottia* has a single species. Thoreaales has two genera: *Nemalionopsis* with two species and *Thorea* with 12 species.

**Keywords** Acrochaetiales · Balbianiales · Eurhodophytina · Florideophyceae · Freshwater · Nemaliophycidae · Rhodophyta · Taxonomy · Thoreaales

### Subclass Nemaliophycidae T Christensen, Bot Tidsskr 73:66 (1978)

The characteristics of the class are as follows (adapted from Kamiya 2017): thalli epilithic, epiphytic, endophytic, or parasitic; pit plugs with two cap layers, with or without cap membrane, outer cap layer dome-shaped in Balbianiales, Balliales, and Batrachospermales and plate-shaped in other orders; life cycle variable: standard triphasic pattern with alternation of heteromorphic or isomorphic generations,

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triphasic pattern producing haploid gametophytes from diploid sporophyte through vegetative meiosis (lack of meiospore production) or biphasic pattern lacking carposporophyte stage; carpogonia sessile on vegetative cells or on 1–2-celled stalks, rarely intercalary, occurring as single cells or with 3–8-celled carpogonial branches; fertilized carpogonia giving rise either directly, or after dividing transversely or longitudinally, to small diploid filamentous carposporophytes with terminal carposporangia; auxiliary cells absent; tetrasporangia (where known) cruciate or irregularly cruciate.

The subclass currently has ten orders: Acrochaetiales, Balbianiales, Balliales, Batrachospermales, Colaconematales, Entwisleales, Nemaliales, Palmariales, Rhodachlyales, and Thoreales. The association among five orders within the Nemaliophycidae (Acrochaetiales, Colaconematales, Entwisleales, Nemaliales, and Palmariales) is well resolved, whereas for the remaining orders it is not well established (Lam et al. 2016). Freshwater members are represented in the Acrochaetiales (primarily marine, except for the genera *Audouinella* and *Ottia*) and the exclusively freshwater orders Balbianiales, Batrachospermales, and Thoreales.

### ***Order Acrochaetiales Feldmann, Proc Int Seaweed Symp 1:11 (1953)***

Members of Acrochaetiales are epilithic, epiphytic or endophytic, marine or freshwater. Thallus is heterotrichous, monosiphonous simple or branched filaments, attached by a single cell or a multicellular prostrate system. Erect filaments are often tufted, with cylindrical to moniliform or irregular in shape, uninucleate cells. Plastids are parietal or axial, discoid, lobed or stellate in shape, single or multiple per cell, without or with one to several pyrenoids. Pit plugs have two cap layers and cap membranes; outer cap layer is thin, plate-like. Monophasic members have reproduction by monospores, biphasic have reduced gametophytes, and triphasic have morphologically similar or dissimilar gametophytes and tetrasporophytes. Carpogonia are sessile on vegetative cells or on one to two-celled stalks, rarely intercalary, without carpogonial branch; fertilized carpogonia giving rise either directly, or after dividing transversely or longitudinally, to small diploid filamentous carposporophytes with terminal carposporangia; auxiliary cells are absent. Spermatangia are borne singly or in clusters on the erect filaments. Tetrasporangia are cruciate or irregularly cruciate.

Freshwater red algae are exclusively in two families, **Audouinellaceae** Woelkerling and **Ottiaceae** JR Evans, ML Vis, and GW Saunders. The Audouinellaceae has a single genus *Audouinella* containing all freshwater species and is characterized by having parietal, band-shaped or laminate plastids, triphasic life history, gametophyte consisting of multicellular base, isomorphic with tetrasporophyte and producing monosporangia (Saunders et al. 2017). The Ottiaceae has a single monospecific genus, *Ottia* and is characterized by having 1–2 reddish-brown parietal plastids without pyrenoids and gametophyte consisting of

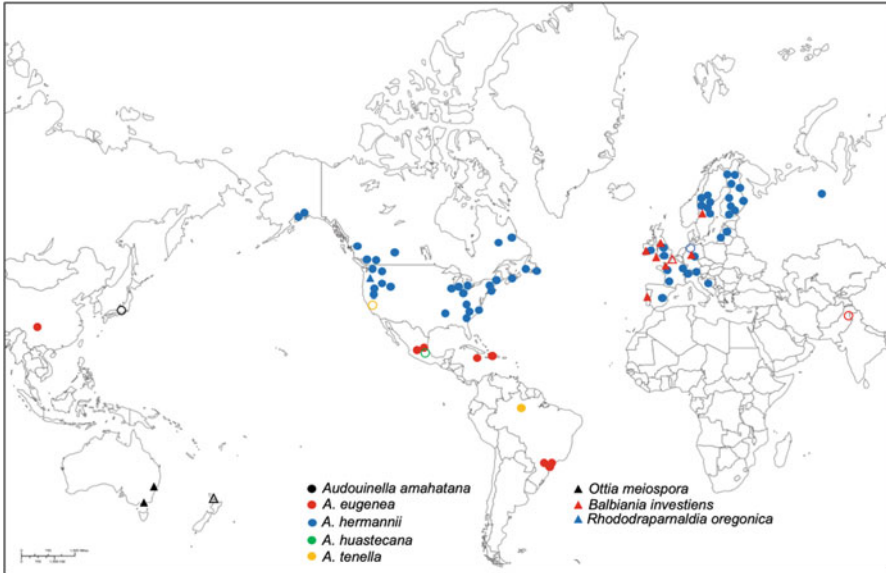
heterotrichous filaments growing intertwined on species of *Nothocladus* s. lat. (Entwisle et al. 2018).

***Audouinella*** Bory, Dictionnaire Classique d'Histoire Naturelle vol 3:341 (1823)

**Type species:** *Audouinella hermannii* (Roth) Duby, Aug Pyrami de Candolle Botanicon Gallicum:972 (1830).

**Description:** thalli filamentous, heterotrichous, uniaxial, reddish, growing typically in dense tufts; basal portion composed of rhizoidal outgrowth, simple or parenchymatous disc; erect filaments consisting of cylindrical cells with unilateral, opposite, or alternate branches; cells contain one to several reddish plastids without pyrenoids; sexual reproduction by spermatangia and carpogonia; spermatangia colorless, arising in clusters on branch tips; carpogonia sessile or stalked, with a cylindrical base and thin trichogyne; distinct carpogonial filament absent; fertilized carpogonia giving rise directly to gonimoblast filaments; carposporophytes spherical to sub-spherical, consisting of a compact mass of short gonimoblast filaments with terminal carposporangia; carposporangia obovoidal to sub-spherical; tetrasporangia single or in clusters, cruciate, formed at branch tips; asexual reproduction by monosporangia are the only known mode of propagation; monosporangia obovoidal, elliptical, spherical, or sub-spherical, arising from short branches on gametophytes or tetrasporophytes.

**Diagnostic characters:** species of *Audouinella* are easily misidentified with the “Chantransia” stage of members of the Batrachospermales and Thoreaales (Skuja 1934; Starmach 1985; Necchi and Zucchi 1997; Zucchi and Necchi 2003), which makes the identification of the true *Audouinella* species problematic. Some criteria based on vegetative morphology were proposed to distinguish *Audouinella* from “Chantransia” stage: color (reddish vs bluish), branching type (regular vs irregular), and monosporangia abundance (abundant vs rare). Species of *Audouinella* are reddish and tend to have a more regular branching, but it is variable and monosporangia can also be abundant in “Chantransia” stages. Among these characters, the only one that has proven to be more generally applicable in studies based on field or cultured specimens is the thallus color with all species of *Audouinella* being reddish (Necchi et al. 1993a) and all “Chantransia” being bluish (Necchi et al. 1993b; Necchi and Zucchi 1997; Zucchi and Necchi 2003). However, “Chantransia” stages of Thoreaales can be brownish (Chiasson et al. 2007), and some species of *Sheathia* can be brownish to reddish in addition to bluish (Han et al. 2020; Vis et al. 2020), which could raise some difficulties in identification. Reproductive characters are also important and when present are more reliable to recognize true *Audouinella* species because in addition to monosporangia they can produce gametangia (carpogonia and spermatangia), carposporophytes, and tetrasporangia, whereas in “Chantransia” stage only monosporangia are produced. However, these reproductive structures are not often observed in field specimens and thus not applicable in many cases. In the absence of reproductive structures other than monosporangia, only reddish populations of freshwater acrochaetoid algae should be interpreted as *Audouinella* and we follow this scheme.



**Fig. 4.1** World map showing the distribution of the species of *Audouinella*, *Ottila*, *Balbiana* and *Rhododraparnaldia*. Open symbols represent the type localities

**Habitat:** species of *Audouinella* occur in a wide range of environmental variables (Necchi et al. 1993a; Carmona and Necchi 2001; Eloranta et al. 2016): *A. huastecana* (temperature 26–27 °C, conductivity 900–1128  $\mu\text{S cm}^{-1}$ , pH 7.0–7.6, current velocity 90–130  $\text{cm s}^{-1}$ ); *A. eugenea* [temperature 19–27(–29) °C, conductivity (130–)310–900(–1237)  $\mu\text{S cm}^{-1}$ , pH (7.0–)7.2–8.3(–8.6), current velocity (9–)21–60  $\text{cm s}^{-1}$ ]; *A. hermannii* [temperature 2–16(–26) °C, conductivity (10–)45–200(–380)  $\mu\text{S cm}^{-1}$ , pH (4.7–)7.4–8.1(–8.7), current velocity (4–)30–81(–130)  $\text{cm s}^{-1}$ ]; *A. tenella* (temperature 8 °C, conductivity 110  $\mu\text{S cm}^{-1}$ , pH 7.6, current velocity 27  $\text{cm s}^{-1}$ ).

**Distribution:** some species have a very restricted distribution (Fig. 4.1) being reported only from the type localities (*A. amahatana* from Japan and *A. huastecana* from Mexico), whereas others are widely distributed on two or three continents (*A. eugenea* from Asia and North and South America, *A. hermannii* from Europe and North America and *A. tenella* from North and South America).

**Phylogenetic relationships among species:** A phylogeny among the species is not feasible because DNA sequences are available only for *A. hermannii*. The three sequences of *A. hermannii* differ in 1.2–2.3% for *rbcL*, with the smallest difference between samples from Canada (New Brunswick) and Ireland and the largest for samples of the USA (North Carolina) and Ireland. Five species are recognized on the basis of morphological characters.

Key to the species of the genus *Audouinella*

1a	Erect system differentiated into proximal and distal parts; proximal cells cylindrical, distal cells barrel-shaped	<i>A. huastecana</i>
1b	Erect system undifferentiated into proximal and distal parts, composed exclusively of cylindrical cells	2
2a	Diameter of vegetative cells $\leq 7 \mu\text{m}$	3
2b	Diameter of vegetative cells $> 7 \mu\text{m}$	4
3a	Tetrasporangia obovoidal, 11–14 $\mu\text{m}$ in length, known from Asia (Japan)	<i>A. amahatana</i>
3b	Tetrasporangia spherical or obovoidal, 8–12 $\mu\text{m}$ in length, known from North and South America	<i>A. tenella</i>
4a	Branch angles $\leq 25^\circ$ , spermatangia $\geq 6 \mu\text{m}$ in diameter	<i>A. eugenea</i>
4b	Branch angles $\geq 25^\circ$ , spermatangia $\leq 6 \mu\text{m}$ in diameter	<i>A. hermannii</i>

***Audouinella amahatana*** (Kumano) Garbary, *Bibl Phycol* 77:19 (1987) (Fig. 4.2a, b)

**Basionym:** *Acrochaetium amahatanum* Kumano, *Jap J Phycol* 26:105 (1978).

**Type:** Kobe University, S Kumano, 1.xi.1973 (Holotype, not found).

**Type locality:** Japan, Yamanashi, Okusawa-dani, tributary of Amahata River, 35.408611° N, 138.331667° E (estimated).

**Description:** thalli microscopic,  $\leq 500 \mu\text{m}$  in height; basal system composed of filaments with fusiform cells, loosely arranged, 5–12  $\mu\text{m}$  in length, 4–6  $\mu\text{m}$  in diameter; erect system with alternate, rarely unilateral branches, branch angles  $\leq 25^\circ$ , composed of filaments with cylindrical cells, 5–15  $\mu\text{m}$  in length, 4–7  $\mu\text{m}$  in diameter; 1 plastid per cell; monosporangia single or in small groups on short lateral branches, obovoidal, 7–10  $\mu\text{m}$  in length, 5–8  $\mu\text{m}$  diameter; tetrasporangia single or in small groups, mixed with monosporangia, on short lateral branches, obovoidal, 11–14  $\mu\text{m}$  in length, 7–9  $\mu\text{m}$  diameter; gametangia and carposporophytes not observed.

**Diagnostic characters:** this species is distinct from others in the genera by the thinner cells of erect filaments ( $\leq 7 \mu\text{m}$  in diameter), which is similar to *A. tenella*. However, it differs by the shape and size of tetrasporangia: obovoidal and longer (11–14  $\mu\text{m}$  in length), whereas in *A. tenella* they are spherical or obovoidal and shorter (8–12  $\mu\text{m}$  in length). In addition, *A. amahatana* is only known from Japan and *A. tenella* occurs in North and South America.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Japan, known only from the type locality (Fig. 4.1).

**Key references:** Kumano (1978), Garbary (1987).

***Audouinella eugenea*** (Skuja) Jao, *Sinensia* 11:362 (1940) (Fig. 4.2c, d)

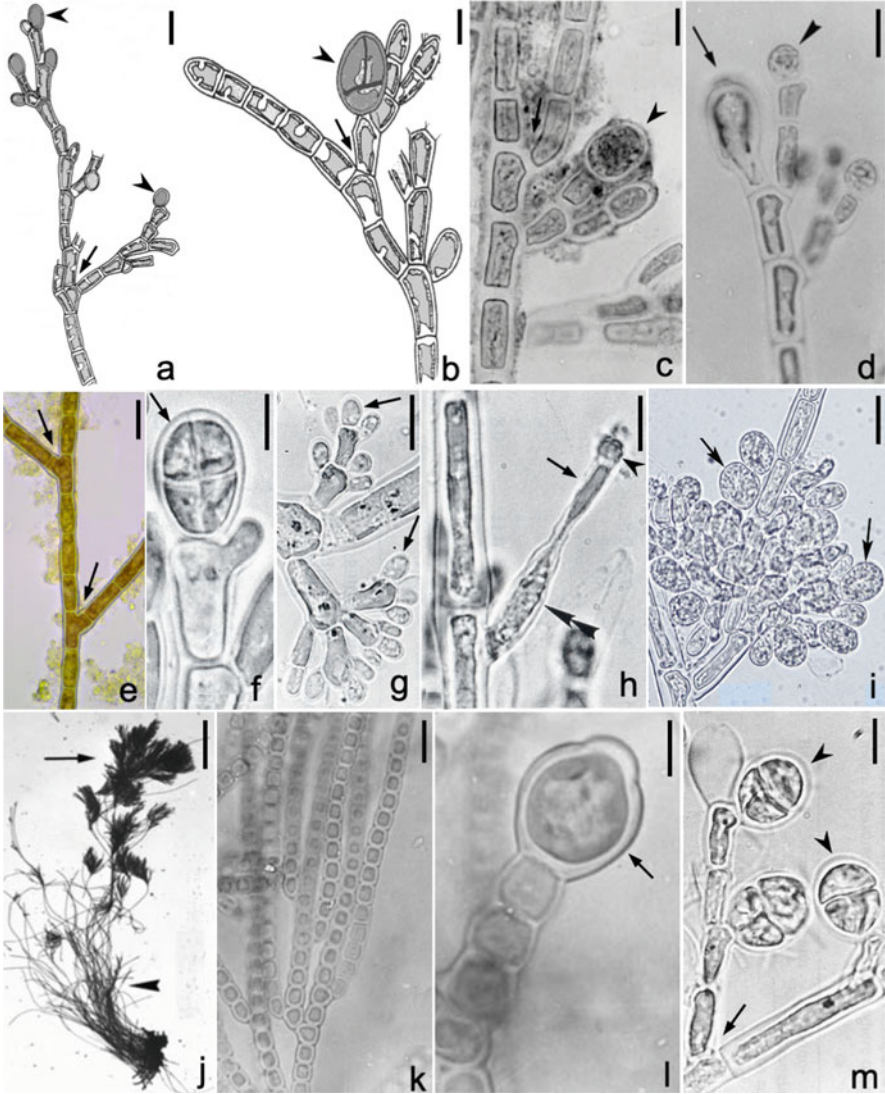
**Basionym:** *Chantransia eugenea* Skuja, *Beih Bot Centralbl* 52:177 (1934).

**Type:** not found.

**Type locality:** Pakistan, Lahore, 31.519904° N, 74.357873° E (estimated).

**Description:** thalli macroscopic,  $\geq 1 \text{ mm}$  in height; basal system composed of irregular prostrate mass with densely aggregated filaments of cylindrical cells;





**Fig. 4.2** (a, b) *Audouinella amahatana*: (a) filament with wide branch angle (arrow) and monosporangia at the tips (arrowheads); (b) filament with wide branch angle (arrow) and tetrasporangia at the tip (arrowhead); (c, d) *A. eugenea*: (c) filament with narrow branch angle (arrow) and monosporangium at the tip (arrowhead); (d) filament with a putative propagule (arrow) and spermatangia at the tip (arrowhead); (e–i) *A. hermannii*: (e) filament with wide branch angles (arrows); (f) tetrasporangium (arrow) at the tip of a branch; (g) spermatangia (arrows) in cluster; (h) trichogyne (arrow) with attached spermatium (arrowhead) and carpogonium (double arrowhead); (i) carposporophyte with carposporangia (arrows); (j–l) *A. huastecana*: (j) general view of a thallus differentiated in proximal (arrow) and distal (arrowhead) parts; (k) filaments of distal part with barrel-shaped cells; (l) monosporangium (arrow) at the tip of a branch; (m) *A. tenella*: (m) filament with wide branch angle (arrow) and tetrasporangia (arrowheads). Scale bars: (j) = 500  $\mu\text{m}$ ; (e, k) = 20  $\mu\text{m}$ ; (a, c, d, g–i) = 10  $\mu\text{m}$ ; (b, f, l, m) = 5  $\mu\text{m}$  (Fig. (c, d) reprinted with permission by Taylor and Francis from Carmona and Necchi (2001); Fig. (f–h) reprinted with permission by E. Schweizerbart'sche Verlagsbuchhandlung from Necchi et al. (1993a); Fig. (i) reprinted with permission by Academic Press from Sheath and Vis (2015))

erect system with alternate or opposite branches, branch angles  $\leq 25^\circ$ , composed of filaments with cylindrical cells, (11.5–)28–63  $\mu\text{m}$  in length, (7.5–)9–15(–18.5)  $\mu\text{m}$  in diameter; 1 plastid per cell; monosporangia single or in clusters on short lateral branches, obovoidal, 12–18  $\mu\text{m}$  in length, (7.5–)9–15(–18)  $\mu\text{m}$  in diameter; spermatangia in groups of 2–3, hyaline, ellipsoidal or obovoidal, 8–12  $\mu\text{m}$  in length, 6–12  $\mu\text{m}$  in diameter; carpogonia, carposporophytes, and tetrasporangia not observed; putative propagules consisting of 1–3 cells, pear-shaped, clavate or irregular, 22–48  $\mu\text{m}$  in length, 16–38  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinct from others in the genus by the thicker cells of erect filaments ( $>7$   $\mu\text{m}$  in diameter), which is similar to *A. hermannii*. However, *A. eugenea* has branching with narrower branch angles ( $\leq 25^\circ$ ) and larger spermatangia ( $\geq 6$   $\mu\text{m}$  in diameter) than *A. hermannii*.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: China, Pakistan; North America: Dominican Republic, Jamaica, Mexico; South America: Brazil (Fig. 4.1).

**Key references:** Skuja (1934), Jao (1940), Necchi et al. (1993a), Carmona and Necchi (2001).

*Audouinella hermannii* (Roth) Duby, Aug Pyrami de Candolle Botanicum Gallicum:972 (1830) (Fig 4.2e–i)

**Basionym:** *Conferva hermannii* Roth, Catalecta Botanica 3:180 (1806).

**Type:** B 28528, L Treviranus (Neotype, designated by Necchi et al. 1993a).

**Type locality:** Germany, near Bremen, 53.079296° N, 8.801694° E (estimated).

**Description:** thalli macroscopic,  $\geq 1$  mm in height; basal system composed of irregular prostrate mass with densely aggregated filaments of cylindrical cells; erect system with alternate or opposite branches, branch angles  $\geq 25^\circ$ , composed of filaments with cylindrical cells, 35–67  $\mu\text{m}$  in length, (7.5–)9–15(–17.9)  $\mu\text{m}$  in diameter; several plastids per cell; monosporangia single or in pairs on short lateral branches, 1–3(–4) cells, obovoidal or sub-spherical, 8–13(–16)  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter; spermatangia in groups of 2–4, terminal, hyaline, ellipsoidal or obovoidal, 4–6  $\mu\text{m}$  in length, 2.8–6  $\mu\text{m}$  in diameter; carpogonia lanceolate or bottle-shaped, with a filiform trichogyne, slightly broader at the distal end, 23–47  $\mu\text{m}$  in length, 3.5–7  $\mu\text{m}$  in diameter; carposporophytes spherical or semi-spherical, dense, (33–)40–80  $\mu\text{m}$  in diameter; carposporangia obovoidal, ellipsoidal, or pear-shaped, (7.5–)9–15(–20)  $\mu\text{m}$  in length, (6–)8–13.5(–16)  $\mu\text{m}$  in diameter; tetrasporangia single or in pairs, terminal on short branches, ellipsoidal or obovoidal, 9.5–14(–17)  $\mu\text{m}$  in length, (6.5–)8–12(–14.5)  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinct from others in the genus by the thicker cells of erect filaments ( $>7$   $\mu\text{m}$  in diameter), which is similar to *A. eugenea*. However, *A. hermannii* has branching with wider branch angles ( $\geq 25^\circ$ ) and smaller spermatangia ( $\leq 6$   $\mu\text{m}$  in diameter) than *A. eugenea*.

**Representative sequences in GenBank:** MH638330 (COI-5P); VU04033, KC134346, MH638328 (*rbcL*).

**Distribution:** Europe: Austria, Britain, Belgium, Croatia, Finland, France, Germany, Ireland, Latvia, Lithuania, Poland, Russia, Slovenia, Spain; North America: the USA and Canada (Fig. 4.1).

**Key references:** Drew (1935), Israelson (1942), Starmach (1985), Necchi et al. (1993a).

**Remarks:** several records of this species from regions other than Europe and North America, where it has been reported with the typical morphology and DNA sequence data, were not considered in the geographic distribution, particularly when the description lacked distinct morphological characters. These records include Africa (Chad, Szinte et al. 2020), Asia (China, Shi et al. 2006; India, Ganesan et al. 2018; Iraq, Maulood et al. 2013; Japan, Hirose and Yamagishi 1977), Australasia (Australia and New Zealand, Skinner and Entwisle 2001), and South America (Brazil, Necchi and Zucchi 1995). Further investigations based on molecular and morphological data are required to reevaluate the records of *A. hermannii* in these regions.

*Audouinella huastecana* JJ Carmona and Necchi, Eur J Phycol 36:221 (2001)  
(Fig. 4.2j–l)

**Type:** FCME PA3261, J Carmona and G Montejano, 9.ix.1989 (Holotype).

**Type locality:** Mexico, San Luis Potosí, Ciudad Valles, Choy, 22.326111° N, 99.086389° W.

**Description:** thalli macroscopic,  $\geq 1$  mm in height; basal system composed of irregular prostrate mass with densely aggregated filaments of cylindrical cells; erect system differentiated into proximal and distal parts; proximal filaments with cylindrical vegetative cells, 16–36  $\mu\text{m}$  in length, 10–16  $\mu\text{m}$  in diameter, unbranched or sparsely branched; distal filaments with barrel-shaped cells, 6–20  $\mu\text{m}$  in length, 6–12  $\mu\text{m}$  in diameter, abundantly branched to form dense fascicles; erect system with alternate or dichotomous branches, branch angles  $\leq 25^\circ$ , rarely at wider angles; 1 plastid per cell; monosporangia in clusters on short lateral branches, 1–3 cells, ellipsoidal or obovoidal, 12–22  $\mu\text{m}$  in length, 10–14  $\mu\text{m}$  in diameter. Gametangia, carposporophytes, and tetrasporangia not observed.

**Diagnostic characters:** this species is unique among species of the genus by having the erect system differentiated into proximal and distal parts: proximal unbranched and with filaments of cylindrical cells, distal branched and with filaments of barrel-shaped cells.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** North America: Mexico (Fig. 4.1).

**Key references:** Carmona and Necchi (2001).

*Audouinella tenella* (Skuja) Papenfuss, Univ Calif Publ Bot 18:326 (1945)  
(Fig. 4.2m)

**Basionym:** *Chantransia tenella* Skuja, Beih Bot Centralbl 52:177 (1934).

**Type:** UC 395493, NL Gardner 3309, v.1916 (Isotype).

**Type locality:** the USA, California, Marin County, Mt. Tamalpais, 37.923544° N, 122.596471° W.

**Description:** thalli macroscopic,  $\geq 1$  mm in height; basal system composed of irregular prostrate mass with densely aggregated filaments of cylindrical cells; erect system with alternate or opposite branches, branch angles  $\geq 25^\circ$ , composed of filaments with cylindrical cells, 14–25.7  $\mu\text{m}$  in length, 3.9–6.1  $\mu\text{m}$  in diameter; 1 plastid per cell; tetrasporangia single or in pairs, spherical (undivided) or obovoidal (after first division), 8–12  $\mu\text{m}$  in length, 7–10.5  $\mu\text{m}$  in diameter; carpegonia, carposporophytes, and monosporangia not observed.

**Diagnostic characters:** this species is distinct from others in the genus by the thinner cells of erect filaments ( $\leq 7$   $\mu\text{m}$  in diameter), which is similar to *A. amahatana*. However, *A. tenella* differs by having spherical (undivided) or obovoidal (after first division) and shorter tetrasporangia (8–12  $\mu\text{m}$  in length) than *A. amahatana* that has obovoidal and longer tetrasporangia (11–14  $\mu\text{m}$  in length). Geographic distribution is also helpful in recognizing these two species: *A. amahatana* is only known from Japan, whereas *A. tenella* is reported from North and South America.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** North America: the USA (California); South America: Brazil (Amazonas) (Fig. 4.1).

**Key references:** Skuja (1934), Necchi et al. (1993a), Necchi and Zucchi (1995).

### Doubtful Species

The reddish species listed below could not be unequivocally recognized as good species in the genus *Audouinella*. Original descriptions were mostly superficial, allowing them to be associated with several species of the genus, and type specimens were not available for checking the diagnostic characters. Some are probably synonyms of species described in the previous section.

***Audouinella desikacharyi*** Ganesan and JA West, *Algae* 28:46 (2013). Based on a literature search, there are no illustrations available for this species and the description given by Desikachary et al. (1990, as *A. pulvinata*) is very wide and could be associated with several species. As stated by Ganesan and West (2013), the treatment of *A. desikacharyi* as a distinct species is made only tentatively, pending critical morphometric and molecular studies on *Audouinella* species known from India. It could be synonymized with *A. eugenea*.

***Audouinella keralaiensis*** (L Jose and RJ Patel) Ganesan and JA West, *Algae* 28:46 (2013). Based on the protologue (Jose and Patel 1990), this species is within the circumscription of *A. eugenea*, also occurring in Asia (China and Pakistan) although no reference was made to that species. While no morphological analysis of diagnostic characters has been made here, there is no basis to recognize it as a distinct species or propose it as a synonym.

***Audouinella lanosa*** Jao, *Sinensia* 12:256 (1941). Based on the protologue (Jao 1941), this species is within the circumscription of *A. eugenea*, also occurring in China, although no reference was made to that species. The character

(monosporangia size) applied by Kumano (2002) to distinguish it from other species showed substantial overlap, particularly *A. eugenea*. While no morphological analysis of diagnostic characters has been made here, there is no basis to recognize it as a distinct species or propose it as a synonym.

All other species referred to *Audouinella* (see Kumano 2002 for descriptions) are bluish forms that most probably represent “Chantransia” stages of Batrachospermales and Thoreaales.

***Ottia*** Entwisle, JR Evans, ML Vis and GW Saunders, J Phycol 54:82 (2017 ‘2018’)

**Type species:** *Ottia meiospora* (Skuja) Entwisle, JR Evans, ML Vis and GW Saunders, J Phycol 54:82 (2017 ‘2018’).

**Description:** thalli filamentous, heterotrichous, uniaxial, reddish-brown to brown, growing endophytic/epiphytic on species of *Nothocladus* s. lat.; basal portion composed of irregularly shaped cells, fusiform or inflated in the middle or ends; erect filaments consisting of obovoid to elongate obpyriform cells with unilateral, opposite, or alternate branches; cells contain one and sometimes two reddish-brown parietal plastids without pyrenoids; sexual reproduction putatively with spermatangia and carpogonia; spermatangia spherical, colorless, on branch tips; carpogonia sessile with a cylindrical base and filiform trichogyne; no carposporophytes observed; monosporangia obovoidal, or sub-spherical, arising in clusters on short branches.

**Diagnostic characters:** *Ottia* like *Audouinella* may be easily misidentified with the “Chantransia” stage of members of the Batrachospermales and Thoreaales. It can be distinguished from “Chantransia” based on having gametangia (carpogonia and spermatangia), whereas “Chantransia” only has monosporangia. In the absence of reproductive structures other than monosporangia, its habit of only growing epiphytic/endophytic on *Nothocladus* s. lat. can also aid in identification.

**Habitat:** no environmental data have been reported.

**Distribution:** this genus is currently known only from Australia and New Zealand (Fig. 4.1).

***Ottia meiospora*** (Skuja) Entwisle, JR Evans, ML Vis, and GW Saunders, J Phycol 54:82 (2017 ‘2018’) (Fig. 4.3a–d).

**Basionym:** *Balbiana meiospora* Skuja, Acta Hort Bot Univ 14:10 (1944).

**Homotypic synonym:** *Audouinella meiospora* (Skuja) Garbary, Biblio Phycol 77: 112 (1987).

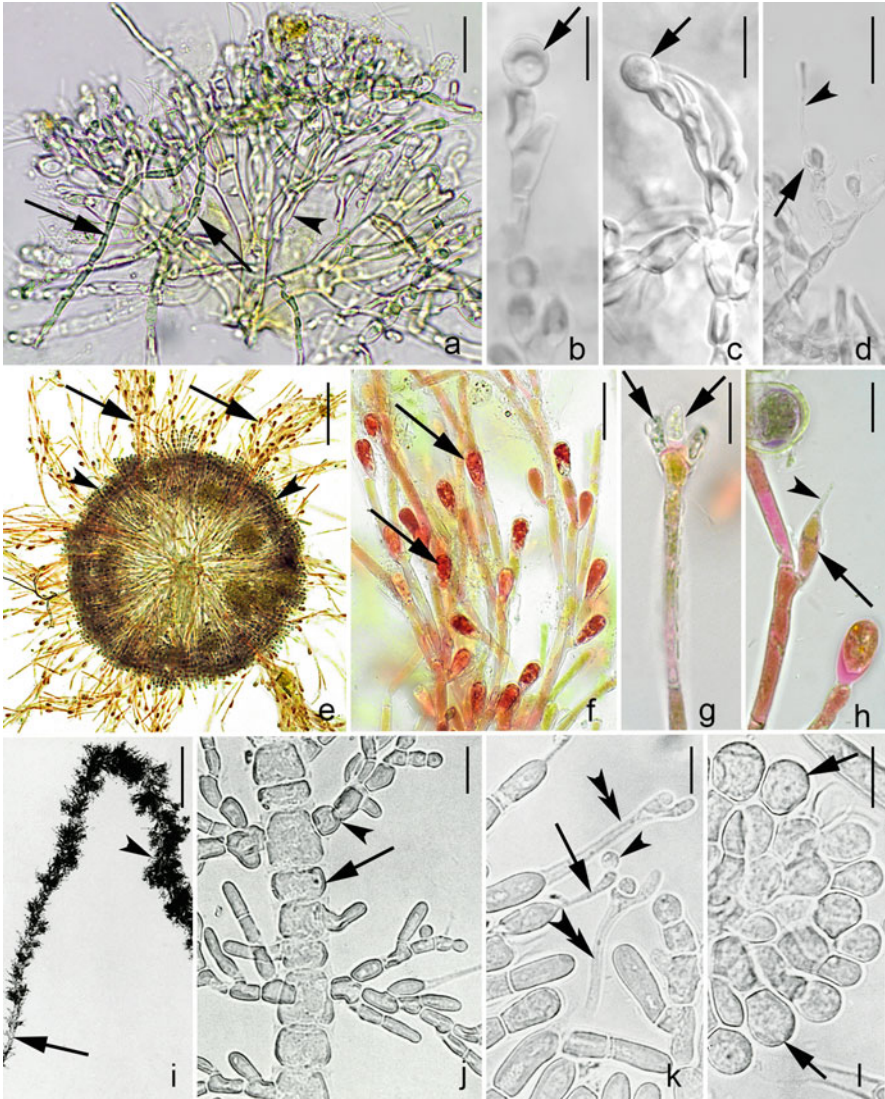
**Type:** NSW 288111–288,115, V Lindauer, 1.xii.1937 (Isolectotypes).

**Type locality:** New Zealand, North Island, Waitangi River near Russell, 35.277744° S, 174.051701° E (estimated).

**Description:** thalli macroscopic, throughout thallus of host; basal system composed of irregular cells, 10–20 µm in length, 2–4 µm in diameter; erect systems with 4–6-celled branches, cells 5–8 µm in length, 4–5 µm in diameter, terminal hairs sometimes present, up to 150 µm in length; spermatangia single or in groups of 2 (–3), 4–5 µm in diameter; carpogonium with filiform trichogyne, 40 µm in length; monosporangia (6–)8–11 µm in length, (5–)7–8 µm in diameter.

**Representative sequences in GenBank:** KY806745 (*rbcL*).





**Fig. 4.3** (a–d) *Ottia meiospora*: (a) general view showing filaments intertwined (arrows) with host (arrowhead) whorl; (b) monosporangium (arrow) at the tip of short branch; (c) spermatangium (arrow) at the tip of a branch; (d) putative carpogonium (arrow) with filiform trichogyne (arrowhead); (e–h) *Balbiana investiens*: (e) general view showing filaments (arrows) growing out of host thallus (arrowheads); (f) monosporangia (arrows) at the tip of branches; (g) spermatangia (arrows) in cluster of three at the tip of elongate cell; (h) carpogonium (arrow) with filiform trichogyne (arrowhead); (i–l) *Rhododraparnaldia oregonica*: (i) general view of thallus with few lateral branches near the base (arrow) and dense branching (arrowhead) in the distal parts; (j) thallus differentiated into large cells (arrow) of main axis and smaller cells (arrowhead) of lateral branches; (k) carpogonium having a filiform trichogyne (arrow) with attached spermatium (arrowhead) and spermatangia at the tips of elongate cells (double arrowheads); (l) carposporophyte with carposporangia (arrows) at the tips; Scale bars: (a, d, f, j) = 25  $\mu\text{m}$ ; (b, c, g, h, k, l) = 10  $\mu\text{m}$ ; (e) = 150  $\mu\text{m}$ ; (i) = 500  $\mu\text{m}$  (Fig. (a–d) reprinted with permission by Wiley from Entwisle et al. (2018). Image author: Fig. (e–h) C Carter; Fig. (i–l) reprinted with permission by Taylor and Francis from Sheath et al. (1994))



**Distribution:** Australasia: Australia (Victoria, New South Wales), New Zealand (North Island) (Fig. 4.1).

**Key references:** Skuja (1944), Entwisle et al. (2018).

**Remarks:** there are records of *Audouinella (Balbiana) meiospora* from Brazil, but not included here since they are from a different continent and on a different host (*Compsopogon*) (Necchi and Zucchi 1995); sequence data are needed to confirm if they belong to this taxon.

### ***Order Balbianiales Sheath and KM Müller, J Phycol 35:863 (1999)***

Members of Balbianiales are freshwater and either epiphytic on *Batrachospermum*-like genera of the Batrachospermales or growing on rock. Thallus is heterotrichous, branched filaments, attached to the substratum by a “Chantransia” stage or unattached intertwining among branches of host. Plastids are parietal, one or two per cell. Pit plugs have two cap layers with no membrane; outer cap layer is domed. A diploid phase of either a tetrasporophyte or “Chantransia.” Carpogonia cylindrical with fusiform trichogyne, sometimes on a short carpogonial branch; fertilized carpogonia giving rise to small diploid filamentous carposporophytes with terminal carposporangia; auxiliary cells are absent. Spermatangia and similar starch-filled cells on a specialized stalk cell. Sporophyte stage either a tetrasporophyte or “Chantransia.” There is only one family **Balbaniaceae** Sheath and KM Müller with the same characteristics as the order.

***Balbiana*** Sirodot, Ann Sci Nat Bot sér 6 3:146 (1876)

**Type species:** *Balbiana investiens* (Lenormand ex Kütz.) Sirodot, Ann Sci Nat Bot sér 6 3:146 (1876).

**Description:** thalli filamentous, heterotrichous, uniaxial, red, monoecious, growing epiphytic on *Batrachospermum*-like genera of the Batrachospermales; filaments consisting of elongate-cylindrical cells with alternate branches; cells contain one and sometimes two parietal band-shaped or discoid plastids; spherical spermatangia on specialized stalked cells; carpogonia on a short lateral branch and having a cylindrical base and filiform trichogynes; carposporophytes composed of gonimoblast filaments with spherical, obovoidal carposporangia at tips; monosporangia obovoidal, arising singly or in pairs on short branches. Tetrasporophyte with cruciate tetrasporangia.

**Diagnostic characters:** this genus can be distinguished from *Rhododraparnadia* based on habit (epiphytic), formation of a typical tetrasporophyte (instead of a

“Chantransia” stage) and geographic distribution in Europe. It is also similar to *Ottia* in morphology and habit (epiphytic) but the geographic distributions differ (Europe and Australasia, respectively).

**Habitat:** this species has only been collected as an epiphyte on *Batrachospermum*-like genera of the Batrachospermales; environmental variables for streams have been reported as follows: pH 6.3–8.1, conductivity 69–206  $\mu\text{S cm}^{-1}$ , water temperature 4–17 °C, mean current velocity 37–43  $\text{cm s}^{-1}$  (Kronborg 1992; Leukart and Knappe 1995; Sheath and Sherwood 2002).

**Distribution:** this genus is currently known only from Europe (Fig. 4.1).

*Balbiania investiens* (Lenormand ex Kütz.) Sirodot, Ann Sci Nat Bot sér 6 3:146 (1876) (Fig. 4.3e–h)

**Basionym:** *Chantransia investiens* Lenormand ex Kützing: Species algarum 431 (1849).

**Type:** PC, Lenormand, 1841, 1843 (numerous specimens attributed to Lenormand—PC0511687, PC0511688, PC0511692–PC0511695).

**Type locality:** France, near Vire, 48.842° N, 0.890° W (estimated).

**Description:** thalli macroscopic, intertwined with thallus of host; branched filaments composed of cells, 30–90  $\mu\text{m}$  in length and 4–9  $\mu\text{m}$  in diameter, terminal hairs sometimes present, up to 150  $\mu\text{m}$  in length; spermatangia on specialized stalk, in clusters of 3–5 cells, 4–5  $\mu\text{m}$  in diameter; carpogonium 4–7  $\mu\text{m}$  in diameter with filiform trichogyne, 15–30  $\mu\text{m}$  in length; carposporophyte with 4–6 celled gonimoblast filaments with apical carposporangia, 14–17  $\mu\text{m}$  in length, 8–9  $\mu\text{m}$  in diameter; monosporangia 15–22  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter. Filamentous tetrasporophyte rarely observed, cells cylindrical, 42–45  $\mu\text{m}$  in length, 4.5–6  $\mu\text{m}$  in diameter.

**Representative sequences in GenBank:** KM055323 (COI-5P), KF944666 (*rbcL*).

**Distribution:** Europe: France, Germany, Portugal, Sweden, the UK (Fig. 4.1).

**Key references:** Sirodot (1876), Swale and Belcher (1963), Leukart and Knappe (1995), Sheath and Sherwood (2002).

**Remarks:** *Balbiania* is treated here as monospecific; however, there are specimens from Brazil (Necchi and Zucchi 1995) and China (Xie and Shi 2004) attributed to *Balbiania meiospora* but not included in *Ottia meiospora*; further investigation is needed to determine which genus these specimens belong or if they represent a new taxon.

*Rhododraparnaldia* Sheath, Whittick and KM Cole, Phycologia 31:1 (1994)

**Type species:** *Rhododraparnaldia oregonica* Sheath, Whittick, and KM Cole, Phycologia 31:1 (1994).

**Description:** thalli macroscopic, crimson red, monoecious, opposite branching with branch cells smaller than main axis cells; attached to substratum by filamentous “Chantransia” phase; spermatangia on long colorless stalks; carpogonia cylindrical at base with a filiform trichogyne sometimes inflated at tip; carposporophyte with short gonimoblast filaments and spherical carposporangia at tips.

**Diagnostic characters:** this taxon can be distinguished from *Balbiana* based on habit (epilithic), the production of a “Chantransia” stage and geographic distribution in Northwest North America.

**Habitat:** it has been found in the following environmental conditions from two locations: pH 8.3, conductivity 30  $\mu\text{S cm}^{-1}$ , water temperature 8–11 °C, mean current velocity 35–61  $\text{cm s}^{-1}$  (Sheath et al. 1994).

**Distribution:** this genus is currently known only from western North America (Fig. 4.1).

*Rhododraparnaldia oregonica* Sheath, Whittick, and KM Cole, *Phycologia* 31:1 (1994) (Fig. 4.3i–l)

**Type:** UBC A80770, RG Sheath, 31.iii.1992 (Holotype).

**Type locality:** the USA, Oregon, HJ Andrews Experimental Forest, Watershed 3 gaging station, 44.218627° N, 122.240995° W (estimated).

**Description:** thalli 6.4–15.1 mm in height, 171–383  $\mu\text{m}$  in diameter; branching opposite with main axis cells 15.1–38.7  $\mu\text{m}$  in length, 17.3–30.1  $\mu\text{m}$  in diameter and branch cells 12.9–21.0  $\mu\text{m}$  in length, 4.3–8.5  $\mu\text{m}$  in diameter; spermatangia stalks 24.2–43.7  $\mu\text{m}$  in length; spermatangia 2.0–4.3  $\mu\text{m}$  in diameter; carpogonium 5.2–7.9  $\mu\text{m}$  in diameter with filiform trichogyne, 19.4–29.3  $\mu\text{m}$  in length; carposporangia 7.4–10.8  $\mu\text{m}$  in length, 5.5–7.9  $\mu\text{m}$  in diameter.

**Representative sequences in GenBank:** AF029156 (*rbcL*).

**Distribution:** North America: the USA, Oregon (two locations) (Fig. 4.1).

**Key references:** Sheath et al. (1994), Sheath and Müller (1999).

**Remarks:** although this taxon was originally collected in two locations in Oregon, subsequent attempts to recollect it in both locations have been unsuccessful.

### *Order Thoreaales KM Müller, Sheath, AR Sherwood and Pueschel, J Phycol 38:819 (2002)*

Members of Thoreaales are epilithic or epiphytic macroalgae in freshwaters. Thallus is multiaxial with an inner medulla and outer assimilatory filaments, branched, attached to surfaces by the filamentous “Chantransia” sporophyte. Plastids are parietal, discoid, or lobed multiple per cell. Pit plugs have two plate-like cap layers and no cap membranes; outer cap layer is thin plate-like. Sexual reproductive structures consisting of spermatangia and carpogonia. Spermatangia are borne singly or in clusters on the erect filaments. Carpogonial branches are few-celled and have apical carpogonia that have a sub-spherical or ovoidal base and thin elongate trichogynes. Fertilized carpogonia give rise directly to gonimoblast filaments. Carposporophytes consist of a compact mass of short gonimoblast filaments with terminal carposporangia. Asexual reproduction via monosporangia arising from long branches on gametophytes or at filament apex for “Chantransia.” There is a single

family, **Thoreaceae** Hassall, with the same characteristics as the order, containing two genera *Nemalionopsis* and *Thorea*.

Key to the genera

1a	Thallus with assimilatory filaments contained in a mucilaginous matrix, reproductive structures near the tips of assimilatory filaments	<i>Nemalionopsis</i>
1b	Thallus with assimilatory filaments not contained in a mucilaginous matrix, reproductive structures at the base of assimilatory filaments	<i>Thorea</i>

*Nemalionopsis* Skuja, Beih Bot Centralb 52:188 (1934)

**Type species:** *Nemalionopsis shawii* Skuja Beih Bot Centralb 52:191 (1934).

**Description:** thalli multiaxial, red, reddish-brown, sometimes branched, resembling fuzzy string; assimilatory filaments embedded in a mucilaginous matrix. Sexual reproduction by spermatangia and carpogonia; spermatangia colorless, sub-spherical to ellipsoidal, terminal or sub-terminal on assimilatory filaments; carpogonia sessile with an ovoidal base and thin trichogynes; carposporangia obovoidal to sub-spherical; monosporangia obovoidal, ellipsoidal, spherical or sub-spherical, arising from long branches on gametophytes or at filament apex for “Chantransia.”

**Diagnostic characters:** this genus is distinct from *Thorea* in having assimilatory filaments embedded in a mucilaginous matrix and reproductive structures are near the tips of the assimilatory filaments.

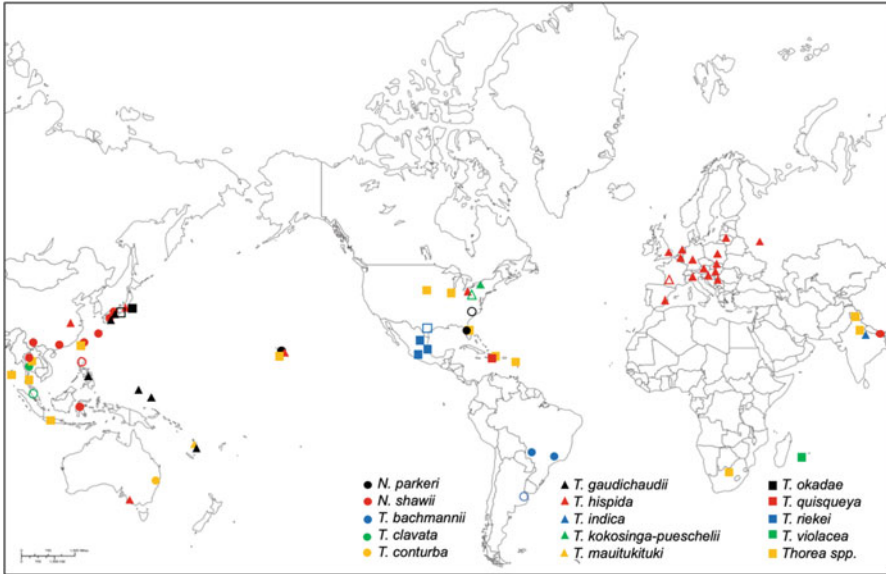
**Habitat:** species of *Nemalionopsis* occur in tropical and temperate regions, but there are few measurements for stream characteristics. *N. parkeri* has been reported from streams with current velocity 29 cm s<sup>-1</sup>, temperature 13–22 °C, pH 7.1–8.3, and conductivity 220 μS cm<sup>-1</sup> (Howard and Parker 1979; Sheath et al. 1993). *N. shawii* has been collected from streams with current velocity 15–20 cm s<sup>-1</sup>, temperature 12–28 °C, pH 8.5, conductivity 60 μS cm<sup>-1</sup> (Migita and Takasaki 1991; Johnston et al. 2014; Necchi et al. 2016).

**Distribution:** species have been reported from a wide geographic distribution (Fig. 4.4). Some reports are based on DNA sequence data from “Chantransia” collected in locations without macroscopic gametophytic thalli and others are from culture collections (Chiasson et al. 2007; Johnston et al. 2018).

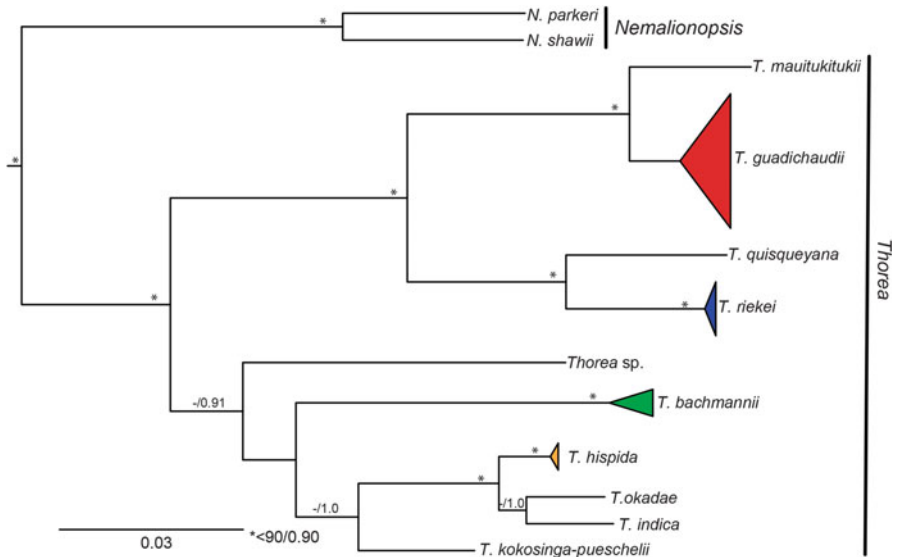
**Phylogenetic relationships among species:** there are two recognized species of *Nemalionopsis* (*N. parkeri* and *N. shawii*) and in a *rbcL* phylogeny with *Thorea*, these two species form a well-supported clade (Fig. 4.5). Although there are sequence data for multiple specimens of each species, intraspecific variation is low (<0.7% *rbcL*).

Key to the species of the genus *Nemalionopsis*

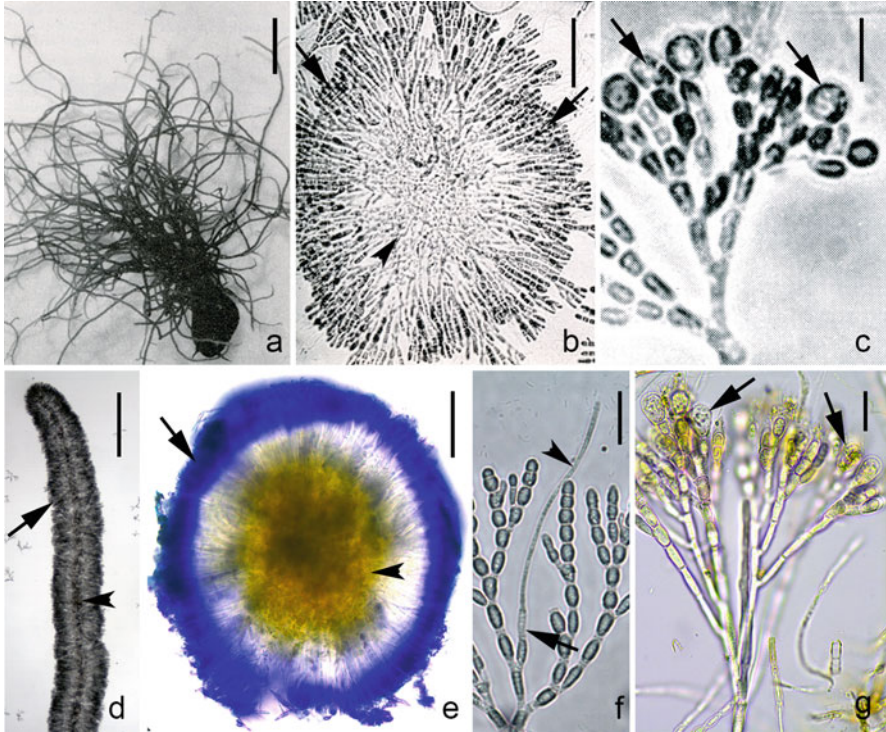
1a	Assimilatory filaments composed of ≤12 cells <144 μm in length; geographic occurrence in North America and Hawaiian Islands	<i>N. parkeri</i>
1b	Assimilatory filaments composed of ≥13 cells and ≥145 μm in length, geographic occurrence in Asia, including southeast Asian islands	<i>N. shawii</i>



**Fig. 4.4** World map showing the distribution of the two species of *Nemalionopsis* and 12 species of *Thorea*. Open symbols represent the type localities. *Thorea* spp. refers to locations where the genus has been reported but the species designation is uncertain by the current criteria; these records do not represent the same species but show the wider geographic distribution of the genus



**Fig. 4.5** Phylogenetic tree of *Nemalionopsis* and *Thorea* species based on *rbcL* sequences. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities



**Fig. 4.6** (a–c) *Nemalionopsis parkeri*: (a) thallus habit; (b) thallus cross section showing outer photosynthetic, compact assimilatory filaments (arrows) and inner medulla (arrowhead); (c) monosporangia (arrows) at the tips of assimilatory filaments; (d–g) *Nemalionopsis shawii*: (d) thallus apex with compact assimilatory filaments (arrow) and narrow inner medulla (arrowhead); (e) cross section assimilatory filaments in a mucilaginous matrix stained blue (arrow) and inner unstained medulla (arrowhead); (f) ovoidal carpogonium base (arrow) with long thin trichogyne (arrowhead) extending past the assimilatory filaments; (g) carposporangia (arrows) at the tips of many-celled gonimoblast filaments. Scale bars: (a) = 10 mm; (b) = 50  $\mu$ m; (c, f, g) = 20  $\mu$ m; (d) = 500  $\mu$ m; (e) = 100  $\mu$ m (Fig. (a–c) reprinted with permission by Taylor and Francis from Howard and Parker (1979))

*Nemalionopsis parkeri* ET Johnston and ML Vis, J Phycol 54:167 (2018)  
(Fig. 4.6a–c)

**Type:** US 60570 (barcode 00165890), RV Howard, 28.ix.1975 (Holotype).

**Type locality:** the USA, North Carolina, Wake County, Lower Barton Creek, Route 1005, 35.959106° N, 78.647677° W (estimated).

**Description:** thalli, reddish-brown, moderately mucilaginous, branched, 10–15 cm in length, 300–400  $\mu$ m in diameter; medulla 111–454  $\mu$ m in diameter; assimilatory filaments up to 144  $\mu$ m in length, composed of 7–12 cells, 7.2–11  $\mu$ m in length, 3.5–6.5  $\mu$ m diameter; spermatangia, carpogonia, and carposporophytes



not observed; monosporangia obovoidal, single or in pairs, at the tips of assimilatory branches, 8–14  $\mu\text{m}$  in length, 7–9  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species has shorter assimilatory filaments with fewer cells than *N. shawii*.

**Representative sequences in GenBank:** KC596318, KM055242 (COI-5P), KM005142 (*rbcL*).

**Distribution:** North America: the USA (Florida, North Carolina) and Pacific Islands: Hawaii (Hawai'i, Mau'i) (Fig. 4.4).

**Key references:** Howard and Parker (1979), Sheath et al. (1993), Johnston et al. (2018).

**Remarks:** in the protologue, the *rbcL* sequence KM005141 from UTEX LB 2737 is stated, but the correct sequence is KM005142 From UTEX LB 2740 (as presented in the supplemental table in Sheath et al. 1993). Sheath et al. (1993) reported *N. tortuosa* from Florida, but this specimen is interpreted to represent *N. parkeri* based on morphology and geographic location.

*Nemalionopsis shawii* Skuja Beih Bot Centralb 52:191 (1934) (Fig. 4.6d–g)

**Type:** NY 945474, WR Shaw and Day #490, 28.iv.1907 (Isotype).

**Type locality:** Philippines: Luzon, Bataan Province, Lamao Forest Reserve, 14.66° N, 120.38° E (estimated).

**Description:** thalli monoecious, dark brown, moderately mucilaginous, branched, 15–50(–100) cm in length, 316–865  $\mu\text{m}$  in diameter; medulla 52–325  $\mu\text{m}$  in diameter; assimilatory filaments 145–390  $\mu\text{m}$  in length, composed of 13–20 cells, 8.5–20  $\mu\text{m}$  in length, 3.5–5.5  $\mu\text{m}$  in diameter; proximal cells cylindrical short to elongate or ellipsoidal; distal cells cylindrical, ellipsoidal, or barrel-shaped; spermatangia 7.0–10.5  $\mu\text{m}$  in length, 4.5–8.0  $\mu\text{m}$  in diameter; carpogonia 2.8–7  $\mu\text{m}$  in diameter, arising from the basal cell of assimilatory filaments or on a one-celled branch with trichogynes 33.2–110  $\mu\text{m}$  in length, 1.4–4  $\mu\text{m}$  in diameter; gonimoblast filaments radially arranged, composed of cylindrical or elongate-cylindrical cells, 10.5–24.5  $\mu\text{m}$  in length, 5.0–7.5  $\mu\text{m}$  in diameter; carposporangia in clusters, obovoidal, 12.5–17.0  $\mu\text{m}$  in length, 9.5–12.0  $\mu\text{m}$  in diameter; monosporangia not observed for gametophyte stage.

**Diagnostic characters:** this species has longer assimilatory filaments with more cells than *N. parkeri*.

**Representative sequences in GenBank:** KX958099, KX958100 (COI-5P), AB159659, KF557550, KU508674 (*rbcL*).

**Distribution:** Asia: China, Indonesia, Japan, Nepal, Philippines, Taiwan, Thailand (Fig. 4.4).

**Key references:** Skuja (1934), Sheath et al. (1993), Necchi et al. (2016), Johnston et al. (2018).

**Remarks:** another species epithet, *N. tortuosa* is common in the literature but currently is regarded as a synonym of *N. shawii* and all records of that species were treated as *N. shawii* here.

*Thorea* Bory, Ann Mus Hist Nat 12:127 (1808)

**Type (Lectotype) species:** *Thorea ramosissima* Bory, Ann Mus d'Hist Nat 12:128 (1808) nom. illeg. (currently accepted name: *T. hispida*).

**Description:** thalli multiaxial, red, reddish-brown, sometimes branched, resembling fuzzy string; assimilatory filaments loose, not embedded in a mucilaginous matrix. Sexual reproduction by spermatangia and carpogonia that are close to the base of the assimilatory filaments; spermatangia colorless, terminal or sub-terminal on assimilatory filaments. Carpogonial branches near the base of the assimilatory filaments, 0–2(–3) short-cylindrical or barrel-shaped cells; carpogonia sessile with an ovoidal or bottle-shaped base and thin, filiform trichogynes; fertilized carpogonia giving rise directly to gonimoblast filaments; carposporophytes spherical to sub-spherical, consisting of a compact mass of short gonimoblast filaments with terminal carposporangia; carposporangia obovoidal to sub-spherical; monosporangia obovoidal, ellipsoidal, spherical or sub-spherical, arising from long branches on gametophytes or at filament apex for “Chantransia.”

**Diagnostic characters:** this genus is distinct from *Nemalionopsis* in having assimilatory filaments loose, not embedded in a mucilaginous matrix and reproductive structures are near the base of the assimilatory filaments.

**Habitat:** in North America, this genus has been collected from streams with alkaline pH (7.0–8.3), warm temperature (18–28 °C), current velocity 24–43 cm s<sup>-1</sup>, and a wide range of conductivity 180–2140 μS cm<sup>-1</sup> (Sheath et al. 1993; Carmona and Necchi 2001). *Thorea hispida* has been reported from rivers with alkaline pH (7.1–8.6), varying temperature (5.1–26 °C), current velocity 40–70 cm s<sup>-1</sup> and high conductivity 314–6300 μS cm<sup>-1</sup> in Europe (Bolpagni et al. 2015 and references there in). For South America, there are a few records from Brazil for *T. bachmannii* (as *T. hispida* or *T. violacea*) with stream pH (7.5–8.1), water temperature (18–21 °C), current velocity 17–93 cm s<sup>-1</sup>, and conductivity 79–970 μS cm<sup>-1</sup> (Necchi and Zucchi 1997; Carmona and Necchi 2001; Johnston et al. 2018). *Thorea gaudichaudii* has been collected from Guam in a stream with pH 8.0, water temperature 28 °C, conductivity 50 μS cm<sup>-1</sup> (Johnston et al. 2018). In Japan, *Thorea* species have been observed in streams with pH 6.6–7.5, water temperature 9.5–28 °C and current velocity 8.1–35.6 cm s<sup>-1</sup> (Higa et al. 2007; Terada et al. 2016; Kozono et al. 2018).

**Distribution:** most species have a very restricted distribution (Fig. 4.4) being reported only from the type localities and a few other locales, whereas two species (*T. hispida* and *T. gaudichaudii*) are widely distributed on two or three continents. There are numerous records of *Thorea* from locations for which the species was not identified or the species to which it should be attributed to is unclear in the current taxonomic scheme; these reports are noted on the map (Fig. 4.4).

**Remarks:** similar to many freshwater red algae, this genus has a simple morphology that is very distinctive at the generic level but differentiating among species using morphological characters has been more difficult. There has been a complicated history of species being placed in synonym, sometimes with more than one

species and also being recognized as distinct (Johnston et al. 2018). Characteristics such as thallus size, amount of branching and number of monosporangia per cluster have been used to differentiate species, but these characters could be influenced by environmental conditions and stage in thallus development as well as not being clearly defined. More research on the reproductive characters is needed, especially carposporangia and monosporangia; these structures are similar in size, shape, and cell density and have been variously interpreted by researchers (Sheath et al. 1993; Johnston et al. 2018). Carmona and Necchi (2001) studying specimens with both structures have shown that carposporangia are in fascicles or clusters whereas monosporangia are not. DNA sequence data have distinguished species that share a similar morphology (Johnston et al. 2018).

**Phylogenetic relationships among species:** *rbcL* sequence data show high support for the genus and one clade of four species, but less support for the relationship among the remaining five species and one unnamed specimen (Fig. 4.5). Within the clade of four species, *T. mauiukitukii* sister to *T. gaudichaudii* and *T. quisqueyana* sister to *T. riekei* are well supported. *Thorea hispida*, *T. okadae*, and *T. indica* are closely related in a well-supported clade, whereas *T. kokosinga-pueschelii*, *T. bachmannii*, and *Thorea* sp. (Hawaii) are on longer branches. The sequence recognized as *Thorea* sp. is genetically distinct, but it was derived from “Chantransia” and no physical specimen exist such that it cannot be formally described according to the nomenclatural rules. *Thorea gaudichaudii* has considerable intraspecific genetic variation relative to the other species (1.2% versus 0.2% *T. hispida*, 0.4% *T. riekei*, and 0.9% *T. bachmannii*) but still within the range to be recognized as a single species. There is a total of 12 species in the genus with nine recognized based on DNA sequence data and three based on morphological characters or geographic distribution.

Key to the species of the genus *Thorea*

1a	Thalli small (no longer than a few millimeters), reproductive structures in middle of assimilatory filaments (somewhat intermediate between <i>Thorea</i> and <i>Nemalionopsis</i> )	<i>T. conturba</i>
1b	Thalli large ( $\geq 4$ cm in length), reproductive structures at the base of the assimilatory filaments	2
2a	Assimilatory filaments clavate (greater cell diameter in the upper part)	<i>T. clavata</i>
2b	Assimilatory filaments non-clavate (equal cell diameter in the upper and basal parts)	3
3a	Geographic distribution in North America	4
3b	Geographic distribution in other continents	6
4a	Occurrence restricted to springs of Texas, the USA, and central Mexico	<i>T. riekei</i>
4b	Occurrence in rivers from temperate regions or tropical streams of Caribbean Islands	5
5a	Widely occurring from midwestern and eastern USA	<i>T. kokosinga-pueschelii</i> and <i>T. hispida</i> (in part) <sup>a</sup>
5b	Restricted to Caribbean Islands	<i>T. quisqueyana</i>

(continued)

6a	Geographic distribution in South America	<i>T. bachmannii</i>
6b	Geographic distribution in Asia, Southeast Asia, and Pacific Islands	7
7a	Geographic distribution restricted to India	<i>T. indica</i>
7b	Geographic distribution restricted to Japan	<i>T. okadae</i>
7c	Geographic distribution restricted to Vanuatu	<i>T. mauiikutukii</i>
7d	Geographic distribution widely occurring throughout Southeast Asia and Pacific Islands	<i>T. gaudichaudii</i> and <i>T. hispida</i> (in part) <sup>a</sup>

<sup>a</sup>*T. hispida* has a wide geographic distribution including the continents of North America and Asia as well as Pacific Islands; it also occurs in Europe, where it is the only species, and Australia

***Thorea bachmannii*** Pujals ex Sheath, ML Vis, and KM Cole, Eur J Phycol 28:232 (1993) (Fig 4.7a, b)

**Type:** BA-C 12709, A Bachman, 27.x.1965 (Lectotype).

**Type locality:** Argentina, Buenos Aires, Arroyo del Gato, La Plata, 34.928226° S, 57.944067° W (estimated).

**Description:** thalli dioecious, abundantly branched, 10–50 cm in length, 400–1300 µm in diameter; medulla 70–320 µm in diameter; assimilatory filaments 140–550 µm in length, composed of 10–18(–21) cells, 15–30 µm in length, 6–11 µm in diameter; proximal cells cylindrical or barrel-shaped; distal cells elongate-cylindrical; male thalli slender compared to female thalli, spermatangia in pairs terminal or sub-terminal on short branches near base of assimilatory filaments, spherical or obovoidal, 8–10 µm in length, 4–7 µm in diameter; carpogonia 5–7 µm in diameter with trichogynes 100–300 µm in length, 2–4 µm in diameter; carposporangia obovoidal, 17–25 µm in length, 8.5–13 µm in diameter.

**Diagnostic characters:** this species is similar in morphology to numerous *Thorea* species; it may be distinguished currently on its geographic distribution in South America which does not overlap any other species and DNA sequence data.

**Representative sequences in GenBank:** KX958092 (COI-5P), KX958138, KX958139 (*rbcL*).

**Distribution:** South America: Argentina, Brazil (Fig. 4.4).

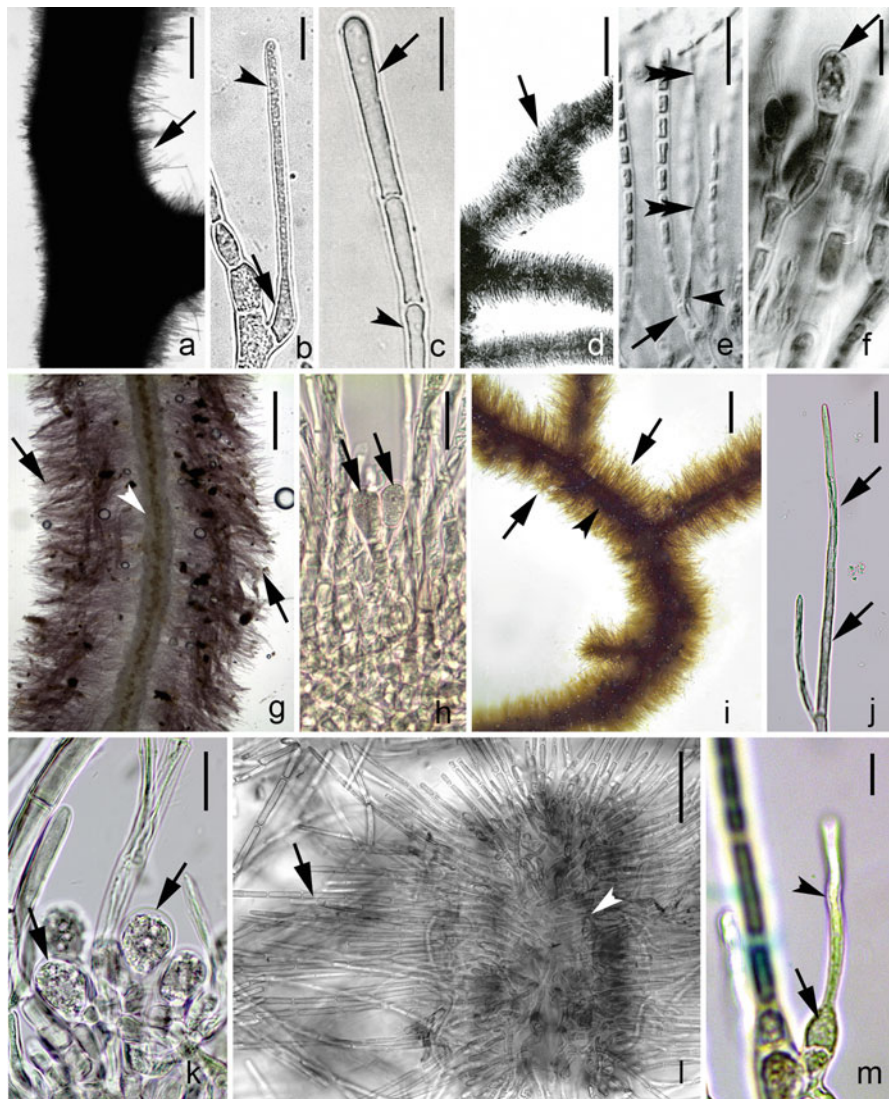
**Key references:** Pujals (1967), Necchi (1987), Necchi and Zucchi (1997), Necchi et al. (2010).

***Thorea clavata*** Seto and Ratnas in Ratnas and Seto, Jap J Phycol 29:248 (1981) (Fig. 4.7c)

**Type:** Private herbarium, M Ratnasabapathy 1218, 6.v.1978 (Holotype), Kobe Coll. Herb. (Isotype, not found).

**Type locality:** Malaysia, Selangor State, Gombak River (19 milestone), 3.322099° N, 101.747846° E (estimated).

**Description:** thalli dull brown, sparsely to moderately branched, length 4.5–10(–12) cm, 480–1425 µm in diameter; medulla 115–420 µm in diameter; assimilatory filaments 130–840 µm in length, composed of (8–)12–25(–40) cells, tapering



**Fig. 4.7** (a, b) *Thorea bachmannii*: (a) thallus with loose assimilatory filaments (arrow); (b) young carpogonium with ovoidal base (arrow) and long, thin trichogyne (arrowhead); (c) *Thorea clavata*: (c) assimilatory filament tapering with wider cell near apex and cells narrowing (arrowhead) towards the filament base; (d–f) *Thorea conturba*: (d) thallus with loose assimilatory filaments (arrow); (e) assimilatory filament (arrow) with carpogonium composed of an ovoidal base (arrowhead) and long, thin trichogyne (double arrowhead); (f) carposporangium (arrow) at the tip of a multi-celled gonimoblast filament; (g, h) *Thorea gaudichaudii*: (g) thallus with loose assimilatory filaments (arrows) and thin medulla (arrowhead); (h) obovoidal carposporangia (arrows) at the base of the assimilatory filaments; (i–k) *Thorea hispida*: (i) thallus with loose assimilatory filaments (arrows) and thick medulla (arrowhead); (j) assimilatory filament composed of cylindrical cells (arrows) that do not narrow towards the base; (k) obovoidal carposporangia (arrows) at the base of the assimilatory filaments; (l, m) *Thorea indica*: (l) thallus with loose assimilatory filaments (arrow) and thick medulla (arrowhead); (m) young carpogonium with ovoidal base (arrow) and long, thin trichogyne (arrowhead). Scale bars: (a) = 500  $\mu\text{m}$ ;



towards the basal part; cells 10–50  $\mu\text{m}$  in length, 2–9  $\mu\text{m}$  in diameter; spermatangia, carpogonia, carposporangia not observed; monosporangia ovoidal, obovoidal, pear-shaped, 8–20  $\mu\text{m}$  in length, 5.5–14  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species can be distinguished from all other species except *T. zollingeri* based on clavate apical cells of the assimilatory filaments and from *T. zollingeri* by having few monosporangia per clusters.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia, Thailand (Fig. 4.4).

**Key references:** Ratnasabapathy and Seto (1981), Johnston et al. (2018).

**Remarks:** new collections of specimens with the salient morphological characters are needed to determine if these characters are phylogenetically informative.

*Thorea conturba* Entwisle and Foard, Phycologia 38:49 (1999) (Fig 4.7d–f)

**Type:** MEL 2045617, TJ Entwisle 2832a, 15.vii.1997 (Holotype); NSW 423887, (Isotype).

**Type locality:** Australia, New South Wales, 25 km northeast of Lismore, tributary of Coopers Creek, Byrangery Creek, 28.62° S, 153.42° E.

**Description:** thalli dioecious, dark brown to green, moderately to abundantly branched, no longer than a few mm, 180–400(–460)  $\mu\text{m}$  in diameter; medulla 48–69  $\mu\text{m}$  in diameter; assimilatory filaments 65–160(–260)  $\mu\text{m}$  in length, composed of 8–18(–30) cylindrical cells, 4–10(–15)  $\mu\text{m}$  in length, 4–7  $\mu\text{m}$  in diameter; spermatangia, usually developing in clusters, ellipsoidal, 10–13  $\mu\text{m}$  in length, 3.5–4  $\mu\text{m}$  in diameter; carpogonia 3–5  $\mu\text{m}$  in diameter, inserted directly on the basal cell of assimilatory filaments or on one discoid or barrel-shaped cell with trichogynes 60–140  $\mu\text{m}$  in length, 2–3  $\mu\text{m}$  in diameter; carposporangia obovoidal, 11–15  $\mu\text{m}$  in length, 6–9  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species has the reproductive structures in the middle of the assimilatory filaments and appears to be a morphology between *Nothocladus* with reproductive structures near the outer portion of the thallus and *Thorea* with structures close to the base of the assimilatory filaments.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia, known only from the type locality (Fig. 4.4).

**Key references:** Entwisle and Foard (1999), Johnston et al. (2018).

**Remarks:** the distinguishing characteristics of this species may be due to its smaller size; *T. hispida* has been confirmed from Australia using DNA sequence data and these data are needed to confirm its unique morphology.



**Fig. 4.7** (continued) (b, f, m) = 10  $\mu\text{m}$ ; (c, e, h, k) = 20  $\mu\text{m}$ ; (d, g) = 250  $\mu\text{m}$ ; (i) = 1 mm; (j, l) = 50  $\mu\text{m}$  (Fig (c) reproduced with permission by the publisher (Taylor and Francis) from Sheath et al. (1993). Fig. (d–f) reprinted with permission by Taylor and Francis from Entwisle and Foard (1999); Image author: Fig. (i) C Carter)



*Thorea gaudichaudii* C Agardh, Systema algarum:56 (1824) (Fig. 4.7g, h)

**Type:** LD 17811, no collector or date (Lectotype designated by Sheath et al. 1993, not found).

**Type locality:** Marianas Islands, no GPS possible with the data provided.

**Description:** thalli reddish-brown, moderately branched,  $\geq 5$  cm in length, 624–1325  $\mu\text{m}$  in diameter; medulla 161–256  $\mu\text{m}$  in diameter; assimilatory filaments 178–628  $\mu\text{m}$  in length, composed of 26–33 cylindrical cells, 14.7–27.7  $\mu\text{m}$  in length, 3.1–6.8  $\mu\text{m}$  in diameter; spermatangia and carpogonia not observed; carposporangia obovoidal, 14.2–23.1  $\mu\text{m}$  in length, 6.8–11.8  $\mu\text{m}$  in diameter; monosporangia obovoidal, 15–20.5  $\mu\text{m}$  in length, 8.9–13.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species has no characteristics to distinguish it from most species of the genus. Its geographic distribution overlaps with *T. mauiitukitukii*, *T. okadae*, and *T. hispida* but not with the other species; it cannot be reliably distinguished from species within its geographic range without DNA sequence data.

**Representative sequences in GenBank:** KM055235, KM055236, KX958106 (COI-5P), AB159649, AB159650, KX958156 (*rbcL*).

**Distribution:** Asia: Japan, Philippines; Pacific Islands: Chuuk, Guam, Vanuatu (Fig. 4.4).

**Key references:** Sheath et al. (1993), Johnston et al. (2018).

**Remarks:** morphometric data include only the measurements from Sheath et al. (1993) (lectotype) and Johnston et al. (2018) (specimens with DNA sequence data). Sheath et al. (1993) reported monosporangia whereas Johnston et al. (2018) reported carposporangia.

*Thorea hispida* (Thore) Desvaux, Observations sur les plantes des environs d'Angers, pour servir de supplément a la flore Maine et Loire, et de suite à l'histoire naturelle et critique des plantes de France:16 (1818) (Fig. 4.7i–k)

**Basionym:** *Conferva hispida* Thore, Magasin Encycl 6:398 (1800).

**Type:** P-JU Herbarium d'Antoine Laurent de Jussieu cat. no, 375-D, J Thore "1801" (Lectotype), BM, L, and MICH673302 (Isolectotypes).

**Type locality:** France, Landes, Dax, Adour River, 43.708608° N, 1.051945° W (estimated).

**Description:** thalli reddish-brown, abundantly branched, up to 100 cm in length, 500–2000  $\mu\text{m}$  in diameter; medulla 88–611  $\mu\text{m}$  in diameter; assimilatory filaments (350–)500–1000(–1400)  $\mu\text{m}$  in length, composed of 15–27 cylindrical cells, 28–49  $\mu\text{m}$  in length, 4.8–8.8  $\mu\text{m}$  in diameter; spermatangia and carpogonia not observed; monosporangia obovoidal, 16.2–21.1  $\mu\text{m}$  in length, 8.0–13.6  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species has no morphological characteristics to distinguish it from most species of the genus. It is the only species known from Europe; its geographic distribution overlaps with *T. mauiitukitukii*, *T. okadae*, and *T. kokosinga-pueschelii*, but not with the other species; it cannot be reliably

distinguished from species within its geographic range without DNA sequence data.

**Representative sequences in GenBank:** KC596320, KX9558095, KX958103 (COI-5P), AB159652, AB159653, KX958142 (*rbcL*).

**Distribution:** Asia: China, Japan; Australasia: Australia; Europe: Austria, Belgium, Croatia, Germany, Hungary, Italy, Lithuania, Netherlands, Poland, Rumania, Russia, Serbia, Slovakia, Spain, the UK; North America: the USA (Ohio), Pacific Islands: Hawaii (Fig. 4.4).

**Key references:** Eloranta et al. (2011), Johnston et al. (2018).

**Remarks:** Johnston et al. (2018) attributed numerous collections to this species using DNA sequence data, but most were “Chantransia,” and no measurements were provided for gametophytes. The distribution shown is based only on records with DNA sequence data or in Europe where only *T. hispida* occurs. Other records such as those from the Caribbean islands in Sheath et al. (1993) are labeled as *Thorea* sp. on the map because they may represent *T. quisqueyana* that is known from the Dominican Republic.

*Thorea indica* Necchi, Ganesan and JA West, *Algae* 30:268 (2015) (Fig 4.7l, m)

**Type:** MEL2389295, K Toppo, 13.iii.2014 (Holotype), SJRP 31508 (Isotype).

**Type locality:** India, Uttar Pradesh, Sai River, 26.650194° N, 80.793972° E.

**Description:** thalli dioecious, dark brown to greenish brown, 4–12 cm in length, moderately to abundantly branched; male thalli slender and abundantly branched, 500–900 µm in diameter; female thalli larger and moderately branched, 700–1250 µm in diameter; medulla 150–400 µm in diameter; short assimilatory filaments 25–45 µm in length, composed of 4–8, short barrel-shaped to cylindrical cells, 5–8 µm in diameter; long assimilatory filaments, sparsely branched, 380–500 µm in length, composed of 10–22 cylindrical cells, 4.5–7.5 µm in diameter; spermatangia arising from the short assimilatory filaments, usually developing in clusters or less often in two, obovoidal or ellipsoidal, 8.5–12.0 µm in length, 5–7.5 µm in diameter; carpogonia 5–9.5 µm in diameter with trichogynes 150–225 µm in length, 2.5–4.5 µm in diameter; monosporangia and carposporangia not observed.

**Diagnostic characters:** this species has no morphological characteristics to distinguish it from most species of the genus. It may be distinguished from other species based on geographic distribution or DNA sequence data.

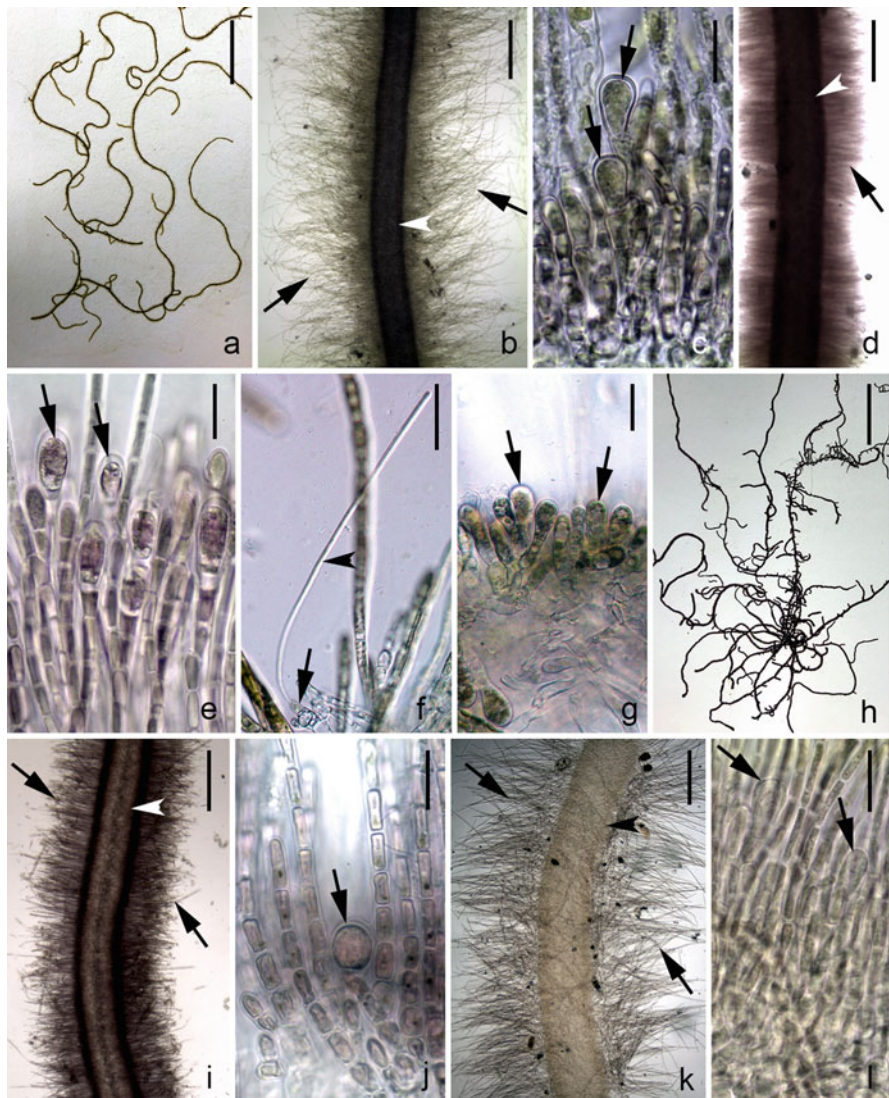
**Representative sequences in GenBank:** KU351644 (COI-5P), KU351645 (*rbcL*).

**Distribution:** Asia: India, known only from the type locality (Fig. 4.4).

**Key references:** Necchi et al. (2015).

**Remarks:** *Thorea* has been reported from other location in India, but it is not yet been determined if specimens from other locations represent this or another species (Ganesan et al. 2018).

*Thorea kokosinga-pueschelii* ET Johnston and ML Vis, *J Phycol* 54:167 (2018) (Fig. 4.8a–c)



**Fig. 4.8** (a–c) *Thorea kokosinga-pueschelii*: (a) thallus habit with few branches; (b) thallus with loose assimilatory filaments (arrows) and thick medulla (arrowhead); (c) obovoidal carposporangia (arrows) at the base of the assimilatory filaments; (d, e) *Thorea mauiutukitukii*: (d) thallus with loose assimilatory filaments (arrows) and thick medulla (arrowhead); (e) carposporangium (arrow) at the tip of a multi-celled gonimoblast filament; (f, g) *Thorea okadae*: (f) carpegonium with ovoidal base (arrow) and long, thin trichogyne (arrowhead); (g) obovoidal carposporangia (arrows) at the base of the assimilatory filaments; (h–j) *Thorea riekei*: (h) thallus habit with numerous branches; (i) thallus with loose assimilatory filaments (arrows) and thick medulla (arrowhead); (j) putative obovoidal carposporangium (arrow) at the base of the assimilatory filaments; (k, l) *Thorea violacea*: (k) thallus with loose assimilatory filaments (arrows) and thick medulla (arrowhead); (l) obovoidal and ellipsoidal carposporangia (arrows) at the base of the assimilatory filaments. Scale bars: (a, h) = 20 mm; (b, d, i, l) = 400  $\mu$ m; (c, e, j) = 20  $\mu$ m; (f) = 50  $\mu$ m; (g) = 25  $\mu$ m; (k) = 250  $\mu$ m (Image author: Fig. (f, g) R Terada)

**Type:** MICH 1210810, R.G. Verb, 12.ix.2011 (Holotype), BHO A-1110 (Isotype).

**Type locality:** the USA, Ohio, Knox County, Kokosing River, 40.372617° N, 82.200531° W.

**Description:** thalli reddish-brown, 8–30 cm in length, abundantly branched, 1130–1453 µm in diameter; medulla 130–310 µm in diameter; assimilatory filaments 441–616.7 µm in length, composed of 12–22(–33) cylindrical cells, 23.3–31.9 µm in length and 5.5–8.3 µm in diameter; spermatangia not observed; carpogonia 5.1–5.5 µm in diameter with trichogynes 65.2–269.7 µm in length, 3.1–5.6 µm in diameter; carposporangia obovoidal, 17–22 µm in length; 10–16 µm in diameter.

**Diagnostic characters:** this species has no characteristics to distinguish it from most species of the genus. Its geographic distribution overlaps with *T. hispida*, but not with the other species but it cannot be reliably distinguished from this species without DNA sequence data.

**Representative sequences in GenBank:** AF506268, KX958150 (*rbcL*).

**Distribution:** North America: the USA (Ohio, New York) (Fig. 4.4).

**Key references:** Johnston et al. (2018).

*Thorea mauiukitukii* ET Johnston, KR Dixon, JA West and ML Vis, J Phycol 54: 168 (2018) (Fig. 4.8d, e)

**Type:** MICH 1210809, R Dixon and K Dixon Kumano, xii.2005 (Holotype).

**Type locality:** Vanuatu, Efate, stream near Eton Beach, 17.738222° N, 168.562283° E (estimated).

**Description:** thalli reddish, 700–958 µm in diameter; medulla 354–362 µm in diameter; assimilatory filaments 177–305 µm in length, composed of up to 17–32 cylindrical cells, 11–15.5 µm in length, 4–5.7 µm in diameter; spermatangia and carpogonia not observed; carposporangia obovoidal, 15–23.9 µm in length, 9.4–11 µm in diameter.

**Diagnostic characters:** this species has no morphological characteristics to distinguish it from most species of the genus. Its geographic distribution overlaps with *T. gaudichaudii*, but not with the other species; it cannot be reliably distinguished from this species without DNA sequence data.

**Representative sequences in GenBank:** KX958113 (COI-5P), KX9558154, KX9558155 (*rbcL*).

**Distribution:** Pacific Islands: Vanuatu, known only from the type locality (Fig. 4.4).

**Key references:** Johnston et al. (2018).

*Thorea okadae* Yamada, Jap J Bot 24:158 (1949) (Fig 4.8f, g)

**Type:** SAP 046883, H. Hirose, 28iii.1939 (Holotype).

**Type locality:** Japan, Kagoshima, Hishikari along Sendai River, 32.018319° N, 130.587706° E (estimated).

**Description:** thalli reddish-brown, up to 1.5 m in length, abundantly branched, 800–1500(–4000)  $\mu\text{m}$  in diameter; medulla 242–395  $\mu\text{m}$  in diameter; short assimilatory filaments up to 150  $\mu\text{m}$  in length, composed of 3–6 cells, 5–18  $\mu\text{m}$  diameter; long assimilatory filaments 150–400  $\mu\text{m}$  in length, composed of 10–15 cylindrical cells, 20–42  $\mu\text{m}$  in length, and 8–14  $\mu\text{m}$  in diameter; spermatangia ovoidal, 10–13  $\mu\text{m}$  in length, 5–6  $\mu\text{m}$  in diameter; carpogonia 6–7  $\mu\text{m}$  in diameter with trichogynes up to 350  $\mu\text{m}$  in length, 3–4  $\mu\text{m}$  in diameter; carposporangia obovoidal, 20–26  $\mu\text{m}$  in length; 13–16  $\mu\text{m}$  in diameter; monosporangia 10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species has no morphological characteristics to distinguish it from most species of the genus. Its geographic distribution overlaps with *T. gaudichaudii* and *T. hispida* but not with the other species; it cannot be reliably distinguished from species within its geographic range without DNA sequence data.

**Representative sequences in GenBank:** KM055238, KX958104 (COI-5P), AB159654, AB159654, KM005139 (*rbcL*).

**Distribution:** Asia: Japan (Fig. 4.4).

**Key references:** Yamada (1949), Yoshizaki (1986), Johnston et al. (2018).

*Thorea quisqueyana* ET Johnston and ML Vis, J Phycol 54:168 (2018)

**Type:** BHO A-0957, R. Thompson, xii.1968, “Chantransia” material from UTEX LB 2743 (Holotype).

**Type locality:** Dominican Republic, La Toma freshwater spring near San Cristobal, 18.457132° N, 70.123626° W (estimated).

**Description:** only known from the “Chantransia” in culture; no gametophytes observed.

**Representative sequences in GenBank:** KM055234 (COI-5P), KM005135 (*rbcL*).

**Distribution:** North America: Dominican Republic, known only from the type locality (Fig. 4.4).

**Key reference:** Johnston et al. (2018).

*Thorea riekei* Bischoff, J Phycol 1:111 (1965) (Fig 4.8h–j)

**Type:** UC1498150, HW Bischoff and GF Papenfuss, 13.xi.1975 (Lectotype here designated).

**Type locality:** the USA, Texas, Comal Co., New Braunfels, 29.709148° N, 98.135284° W (estimated).

**Description:** thalli dark red, up to 2 m in length, sparsely branched, 500–900  $\mu\text{m}$  in diameter; medulla 195–271  $\mu\text{m}$  in diameter; assimilatory filaments, unbranched, 186–408(–775)  $\mu\text{m}$  in length, composed of 25–45 cylindrical cells, 12–40  $\mu\text{m}$  in length, 3.9–7  $\mu\text{m}$  in diameter; spermatangia and carpogonia not observed; carposporangia obovoidal, 11.5–19.8  $\mu\text{m}$  in length, 8.3–12  $\mu\text{m}$  in diameter; monosporangia single or in clusters, obovoidal, spherical, ellipsoidal, 12–15  $\mu\text{m}$  in length, 8–9  $\mu\text{m}$  in diameter.



**Diagnostic characters:** this species has no morphological characteristics to distinguish it from most species of the genus, but its geographic distribution does not overlap with the other species and can be useful to distinguish it.

**Representative sequences in GenBank:** KM055239, KX958107, KX958109 (COI-5P), AB159656, KX958149, KX958151 (*rbcL*).

**Distribution:** North America: the USA, Mexico (Fig. 4.4).

**Key references:** Bischoff (1965), Johnston et al. (2018).

**Remarks:** sporangia were interpreted as monosporangia in Bischoff (1965) and carposporangia in Johnston et al. (2018). Records of *T. hispida* from Carmona and Necchi (2001) have been included here as *T. riekei* based on morphological similarity and geographic distribution of species given in Johnston et al. (2018).

*Thorea violacea* Bory, Ann Mus Hist Nat 12:133 (1808) (Fig. 4.8k, l)

**Type:** BM000770128, JB Bory, 1801–1802, (Lectotype designated in Sheath et al. 1993), PC0602800, PC0602801 (Isotypes).

**Type locality:** Réunion, riviere des Ramparts, 21.313831° S, 55.623500° E (estimated).

**Description:** thalli reddish-brown, sparsely branched, 993–1878 µm in diameter; medulla 218–304 µm in diameter; assimilatory filaments, 291–533 µm in length, composed of up to 60 cylindrical cells, 24.9–32.9 µm in length, 3.5–7.2 µm in diameter; spermatangia not observed; carpogonia 2.4–6.7 µm in diameter with trichogynes 14.7–56.1 µm in length; carposporangia obovoidal, 7.4–19.3 (mean 17.4) µm in length, 5.4–18.1 (mean 8.4) µm in diameter; monosporangia 16.2–24.5 µm in length 7.4–14.1 µm in diameter.

**Diagnostic characters:** this species has no characteristics to distinguish it from most species of the genus. However, its geographic distribution does not overlap with the other species and can be helpful in distinguishing it.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Africa: Réunion, known only from the type locality (Fig. 4.4).

**Key references:** Sheath et al. (1993), Johnston et al. (2018).

**Remarks:** numerous species and specimens from distant geographic locations have been attributed to this species, but DNA sequence data have shown at least some of those are unique. For example, *T. okadae*, *T. riekei*, *T. bachmannii*, and *T. gaudichaudii* had been previously been placed in synonym with *T. violacea* (Sheath et al. 1993), but more recently they have been showed to be genetically distinct from each other (Johnston et al. 2018). Those researchers suggested that trapezoidal basal cells are unique to this species, but that has yet to be established photographically; the type location is geographically distant from other species and DNA sequence data are needed to confirm whether it should continue to be recognized as a distinct species. Note that sporangia were interpreted as monosporangia by Sheath et al. (1993) and as carposporangia by Johnston et al. (2018).



## Doubtful Species

***Thorea brodensis*** Klas, Hedwigia 75:283 (1936). This species is only known from the type locality in Europe. The protologue is confusing providing morphological measurements for summer and winter forms. This species was included in Kumano (2002) based on the greater measurements for the summer form. Sheath et al. (1993) considered it a synonym of *T. violacea* but since that species is currently recognized only from the type locality on the island of Réunion, that synonym is unlikely based on geographic distribution. It is most likely a synonym of *T. hispida*, currently the only species recognized in Europe.

***Thorea flagelliformis*** Zanardini, Mem Reale Inst Ven Sci, Let Art 17:148 (1872). There is a very short description provided in the protologue which cannot be used to assess whether it is distinct based on morphology and there has been no study or report of this species since the protologue. The type location in southeast Asia (Sarawak) is a region of high species diversity for this genus and therefore no synonym can be suggested based on biogeography.

***Thorea prowisei*** Ratnas and Seto, Jap J Phycol 29:246 (1981). This species is only known from the type locality. In the protologue, it was distinguished from *T. gaudichaudii* by having thicker clusters of monosporangia. However, the number of monosporangia or carposporangia in a cluster varies considerably within and among species such that it is not a good taxonomic character. DNA sequence data should be obtained to determine if these species are synonymous since there are numerous species in Southeast Asia and Pacific Islands only distinguished by genetic variation.

***Thorea siamensis*** S Traichaiyaporn and Kumano, Nat Hist J Chulalongkorn Univ 8: 28 (2008). This species is only known from the type locality. In the protologue, it was distinguished from *T. gaudichaudii* based on smaller carposporangia but measurements of *T. gaudichaudii* in Johnston et al. (2018) overlap (16–19 × 8–9 µm in *T. siamensis* and 14.2–23.1 × 6.8–11.8 µm in *T. gaudichaudii*). DNA sequence data should be obtained to determine if these species are synonymous since there are numerous species in Southeast Asia and Pacific Islands only distinguished by genetic variation.

***Thorea zollingeri*** F Schmitz, Ber Deut Bot Ges 10:134 (1892). This species is named from material collected in Java and has not been reported since. Sheath et al. (1993) examined the type specimen and determined that it had clavate assimilatory filaments like *T. clavata* and differed from that species based on the number of monosporangia per cluster. However, the assimilatory filament shown is not convincingly clavate [Fig. 12 in Sheath et al. (1993)] and the number of monosporangia per cluster varies within and among species. Southeast Asia is a region with numerous species having similar morphology such that it would be difficult to determine to which it might be synonymous.

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# Chapter 5

## Subphylum Eurhodophytina, Class Florideophyceae, Subclass Nemaliophycidae, Order Batrachospermales



Morgan L Vis and Orlando Necchi Jr

**Abstract** The order Batrachospermales of the subclass Nemaliophycidae is composed of exclusively freshwater members. This order is comprised of 21 genera and houses more than two-thirds of the freshwater species diversity for the Rhodophyta. Seven of the genera (*Acrocarposporophycos*, *Genadendalia*, *Lympha*, *Notohesperus*, *Petrohua*, *Psilosiphon*, and *Tuomeya*) are monospecific. *Kumanoa* is the most diverse with 41 species. *Sheathia*, *Nothocladus*, and *Paludicola* each have 15 or more species, whereas the other genera have a more modest number from three to nine. Two new genera (*Genadendalia* and *Notohesperus*) are proposed as well as new species in *Paralemanea*, *Lemanea*, and *Torularia*. Although *Balliopsis* and “*Chantransia azurea*” have been shown to be unique lineages within the order, they are not described in the chapter because they most likely represent “*Chantransia*” stages.

**Keywords** Batrachospermaceae · Batrachospermales · Eurhodophytina · Florideophyceae · Freshwater · Nemaliophycidae · Rhodophyta · Taxonomy

### Introduction

Classification information for the subclass Nemaliophycidae was provided in the previous chapter. Within this subclass, freshwater taxa are present in four (Acrochaetiales, Balbianiales, Batrachospermales, and Thoreaales) of the ten orders. The order Batrachospermales is strictly freshwater and has the greatest number of genera and species.

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## ***Order Batrachospermales Pueschel and KM Cole, Am J Bot 69: 717 (1982)***

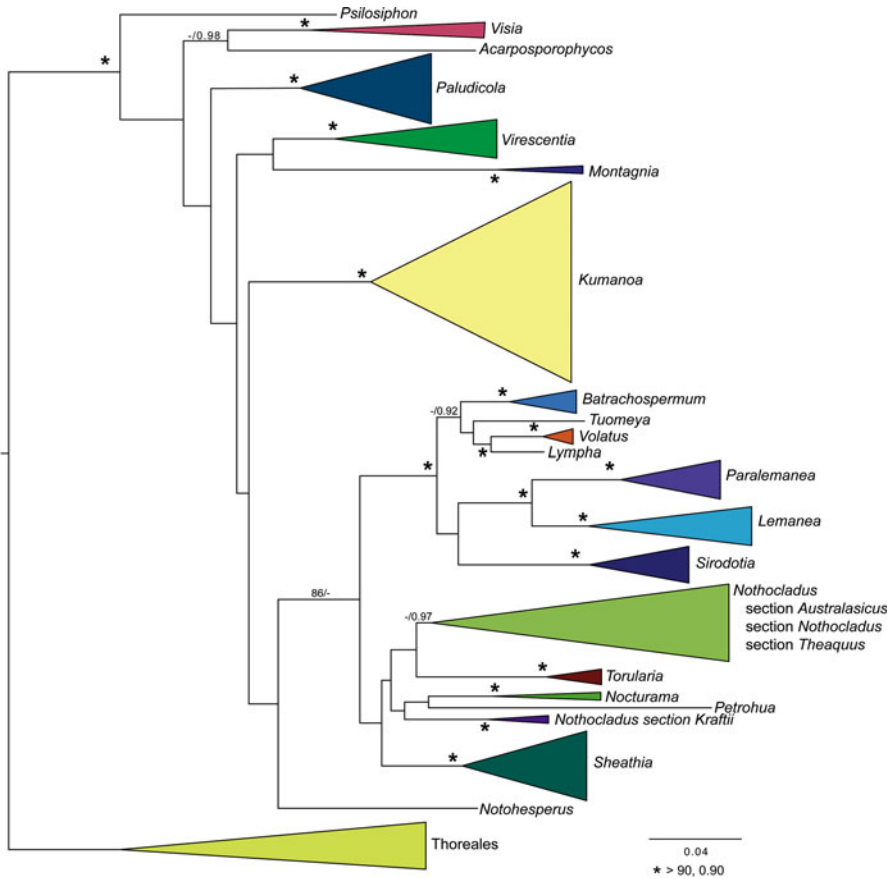
Members of Batrachospermales are strictly freshwater. Macroscopic gametophytic thalli are uniaxial, with whorls of branches giving a bead-like appearance or forming a pseudoparenchymatous thallus, with mucilaginous or cartilaginous consistency. Plastids are parietal discoid or lobed, multiple per cell, without pyrenoids. Pit plugs have two cap layers and cap membranes; outer cap layer is enlarged and dome shaped. Most members have a heteromorphic triphasic life history, and one member (*Acarposporophycos*) is biphasic lacking a carposporophyte. Carpogonia are on a long or short carpogonial branch; fertilized carpogonia give rise directly to small or large diploid carposporophytes with either determinate or indeterminate gonimoblast filaments that have terminal carposporangia. Spermatangia are borne singly or in clusters at the tips of fascicle filaments or in papillae and rings in some pseudoparenchymatous taxa (*Lemanea* and *Paralemanea*). No tetrasporophytes present but instead a filamentous branched diploid phase called “Chantransia” that is morphologically similar to *Audouinella* reproducing asexually via monosporangia and gives rise to the gametophytes through vegetative meiosis.

### ***Phylogenetic Relationships of the Batrachospermales***

Analyses of *rbcL* sequence data show that the Batrachospermales is a well-supported monophyletic group (Fig. 5.1). Twenty of the 21 genera are represented, and most are monophyletic with high support values. In this analysis, the genus *Nothocladus* was paraphyletic with *Nothocladus* section *Kraftii* separate from the other sections. Although the genera were well supported, the relationships among genera generally are unsupported and more research is needed. DNA sequence data support the recognition of a new genus *Notohesperus*. Although *Balliopsis* and “*Chantransia azurea*” have been shown to be unique lineages (not shown in figure) within the order, they are not described in the chapter because they most likely represent “Chantransia” stages (Saunders and Necchi 2002; Szinte et al. 2020). The genus *Genadendalia*, lacking DNA sequence data, can be recognized based on unique morphology of the carposporangia. Comparison of the morphological features for most genera provides a suite of characters by which they can be identified (Table 5.1). However, not all genera can be easily distinguished based on morphology, and DNA sequence data are sometimes necessary such as for *Batrachospermum*, some species of *Sheathia* and *Nothocladus* section *Kraftii*. Some genera have well-defined geographic distributions that may be used as a secondary character.

#### **Family Batrachospermaceae C Agardh, Systema algarum:xxiii (1824)**

This family was amended to include all genera of the Batrachospermales (Entwisle et al. 2009). The description is the same as the order.



**Fig. 5.1** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the genera in the Batrachospermales. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

### Monospecific Genera: *Acarposporophycos*, *Genadendalia*, *Lympha*, *Notohesperus*, *Petrohua*, *Psilosiphon*, and *Tuomeya*

*Acarposporophycos* Necchi, Phytotaxa 395:55 (2019b)

**Synonyms:** *Batrachospermum* subgenus *Acarposporophytum* Necchi, Rev Bras Biol 47:446 (1987); *Batrachospermum* section *Acarposporophytum* (Necchi) Entwisle, ML Vis, WB Chiasson, Necchi and AS Sherwood, J Phycol 45: 713 (2009).

**Type species:** *Acarposporophycos brasiliensis* (Necchi) Necchi and AS Garcia, Phytotaxa 395:56 (2019b).

**Table 5.1** Comparative characters of the genera in the order Batrachospermales

Genus	Consistency	Thallus construction	Carpogonial branch	Carpoporophyte position and size	Unique characters
<i>Acarposporophycos</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Lacking	Lack of carpoporophyte
<i>Batrachospermum</i>	Mucilaginous	Bead-like, without outer cortex	Long, straight	Pedunculate, small	Most species lacking secondary fascicles
<i>Genadendalia</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	Zonate, septate carpoporangia
<i>Kumanoa</i>	Mucilaginous	Bead-like, without outer cortex	Short or long, spiraled or twisted	Axial, large	
<i>Lemanea</i>	Cartilaginous	Pseudoparenchymatous, with outer cortex	Short, mostly straight	Inside thallus	Cortical cells decreasing in size towards periphery; most species with spermatangia in circular papillae
<i>Lympha</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	Reduced whorls; endemic to the USA
<i>Montagnia</i>	Mucilaginous	Bead-like, without outer cortex	Long, straight	Pedunculate, small	Carpogonial branch with enlarged pit-connections after fertilization
<i>Nocturama</i>	Mucilaginous	Bead-like, without outer cortex	Short or long, straight	Pedunculate or short-pedunculate, small	
<i>Nothocladus</i> section <i>Australasica</i>	Mucilaginous or cartilaginous	bead-like, without outer cortex	Short or long, straight	Pedunculate, large, small	
<i>N.</i> section <i>Kraffii</i>	Mucilaginous	Bead-like, without outer cortex	Long, straight	Pedunculate, small	
<i>N.</i> section <i>Nodosus</i>	Cartilaginous	Bead-like, without outer cortex	Short or long, spiraled or twisted	Diffuse, near the outside of whorl	Only identified based on a combination of characters known from other genera and geographic range
<i>N.</i> section <i>Theaquus</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	

<i>Nothocladus</i> no section designated	Mucilaginous	Bead-like, without outer cortex	Short or long, straight	Axial, large, Short-pedunculate, small	
<i>Nothoesperus</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	
<i>Paludicola</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	Two types of gonimoblast filaments (erect and prostrate)
<i>Paralemanea</i>	Cartilaginous	Pseudoparenchymatous, with outer cortex	Short, mostly straight	Inside thallus	Outer cortical cells decreasing in size towards periphery; spermatangia in rings
<i>Petrohata</i>	Cartilaginous	Pseudoparenchymatous, with outer cortex	Putatively short, straight	Inside thallus	Outer cortical cells similar in size; endemic to South America
<i>Psilosiphon</i>	Cartilaginous	Pseudoparenchymatous, with outer cortex	Unknown	Unknown	Outer cortical cells similar in size; endemic to Australia and New Zealand
<i>Sheathia</i>	Mucilaginous	Bead-like, without outer cortex	Long, straight	Pedunculate, small	Many species with heterocortication; secondary fascicles few or absent
<i>Sirodotia</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight or slightly curved	Diffuse, along the axis	Protuberance on one side of carpogonium; prostrate gonimoblast filaments
<i>Torularia</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight or slightly curved	Axial, large	Reduced whorls, autouinelloid fascicles
<i>Tuoneya</i>	Cartilaginous	Pseudoparenchymatous, with outer cortex	Short, spiralled or contorted	Axial, large	Outer cortical cells decreasing in size towards periphery
<i>Virescentia</i>	Mucilaginous	Bead-like, without outer cortex	Short, straight	Axial, large	Long and stalked trichogynes
<i>Visia</i>	Mucilaginous	Bead-like, without outer cortex	Long, straight	Pedunculate, small	
<i>Volatus</i>	Mucilaginous	Bead-like, without outer cortex	Short, contorted or curved	Axial, large	

**Description:** thalli monoecious; blue-greenish, consistency mucilaginous; branching irregular; whorls well developed, contiguous, barrel-shaped or spherical; cortication of the main thallus axis well developed with filaments of cylindrical cells; primary fascicles straight, formed by cylindrical, ellipsoidal, obovoidal, or sub-spherical cells; secondary fascicles abundant and covering the entire internode; spermatangia spherical or obovoidal, terminal or sub-terminal on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, straight, short, developing from the periaxial of primary fascicles, composed of disc- or barrel-shaped cells; involucrel filaments composed of 1–3 ellipsoidal or fusiform proximal cells and usually 1–2 clavate upper distal cells forming a rosette around the carpogonia; carpogonia with sessile, clavate or obovoidal trichogynes; fertilized carpogonia and subtending cells of carpogonial branches with enlarged pit connections ( $>3 \mu\text{m}$  wide); fertilized carpogonia germinate to directly form the filaments of the “Chantransia” stage which grow on the old gametophyte; initial filaments arising coiled around the fertilized carpogonium and later forming upright filaments; carposporophytes one-celled, consisting of the fertilized carpogonia.

**Diagnostic characters:** this genus resembles *Montagnia* in having well-developed whorls, short carpogonia, presence of upper distal cells of involucrel filaments forming a rosette around the carpogonia and cells of post-fertilized carpogonial branches with enlarged pit connections. However, it is unique lacking a carposporophyte and having fertilized carpogonia germinating to directly form the filaments of the “Chantransia” stage that grow on the old gametophyte.

**Habitat:** the species was collected in two rivers with black water (yellow to dark brown color) in partial shade, epilithic on rocky bottom. In one site, *A. brasiliensis* was collected in the following environmental conditions (unpublished data): mild water temperature  $18.3 \text{ }^\circ\text{C}$ , low conductivity ( $5 \mu\text{S cm}^{-1}$ ), slightly acidic pH 6.2, high dissolved oxygen ( $9.1 \text{ mg L}^{-1}$ ), moderate current velocity ( $40 \text{ cm s}^{-1}$ ), partly shaded stream segment in the Atlantic Rainforest.

**Distribution:** this genus is currently known from South America (Fig. 5.2).

*Acarposporophycos brasiliensis* (Necchi) Necchi and AS Garcia, Phytotaxa 395:56 (2019b) (Fig. 5.3a–d)

**Basionym:** *Batrachospermum brasiliense* Necchi, Braz J Biol 47:442 (1987).

**Type:** SP187180, O Necchi Jr, A Custodio Fo, 13.iii.1984 (Holotype); Isotype SJRP 29709.

**Type locality:** Brazil, São Paulo State, Biritiba Mirim, Boracéia Biological Station, Claro River, Pilões,  $23.636127^\circ \text{ S}$ ,  $45.832581^\circ \text{ W}$ .

**Description:** whorls 330–690  $\mu\text{m}$  in diameter; primary fascicles with 6–10 cells; spermatangia 5–7  $\mu\text{m}$  in diameter; carpogonial branches with 3–6 cells, 15–35 (–45)  $\mu\text{m}$  in length; carpogonia 30–50  $\mu\text{m}$  in length, 10–15  $\mu\text{m}$  in diameter.

**Representative sequences in GenBank:** MH917719 (COI-5P); MH917724 (*rbcL*).



**Fig. 5.2** World map showing the distribution of monospecific genera *Acarposporophycos*, *Genadendalia*, *Lympa*, *Notohesperus*, *Petrohua*, *Psilosiphon*, and *Tuomeya*. Open symbols represent the type localities

**Distribution:** South America: Brazil (southeastern) (Fig. 5.2).

**Key references:** Necchi (1987), Necchi et al. (2019b).

***Genadendalia*** ML Vis and Necchi **gen. nov.**

**Type species:** *G. breutelii* (Rabenhorst) ML Vis and Necchi.

**Synonym:** *Batrachospermum* section *Gonimopropagulum* Sheath and Whittick, *Phycologia* 34:38 (1995).

**Description:** thalli monoecious, bluish or olive-green; branching irregular; whorls reduced, loose, elongate pear-shaped, obconical or barrel-shaped, contiguous, indistinct in older parts; cortical filaments of the main axis well developed with cylindrical cells; primary fascicles with cells ranging from cylindrical or ellipsoidal to obovoidal or sub-spherical; secondary fascicles very abundant, covering the entire internode; spermatangia obovoidal or sub-spherical, terminal or sub-terminal on primary or secondary fascicles; carpogonial branches straight, short, arising from the pericentral cells; involucrel filaments short or long; carpogonia with stalked or unstalked, clavate trichogynes; carposporophyte one per whorl, large, axial, sub-spherical; gonimoblast filaments composed of cylindrical cells; carposporangia obovoidal or ellipsoidal, zonately septated forming chambers.





**Fig. 5.3** (a–d) *Acarposporophycos brasiliensis*: (a) barrel-shaped whorls; (b) mature carpogonium with clavate trichogyne (arrow) and distal cells of involucre filaments forming a rosette around the carpogonium (arrowheads); (c) Upright filaments of the “Chantransia” stage (arrows) developing from the coiled filaments (arrowheads) around the fertilized carpogonium; (d) Filaments of the “Chantransia” stage (arrows) developing from the gametophyte. (e–l) *Genadenalia breutelii*: (e) reduced whorls; (f) primary fascicle; (g) fertilized carpogonium with clavate trichogyne (double arrowhead) and attached spermatia (arrowheads); (h) fertilized carpogonium with attached spermatium (arrow) and gonimoblast initial (arrowhead); (i) carposporophyte with large septated carposporangia (arrowheads); (j) germinating carposporangium (arrowhead) with “Chantransia” stage filaments (double arrowheads); (k, l) carposporangia with 4 and 5 chambers. Scale bars: (a, e) = 250  $\mu\text{m}$ ; (d) = 100  $\mu\text{m}$ ; (c, f, i–l) = 50  $\mu\text{m}$ ; (g, h) = 25  $\mu\text{m}$ ; (b) = 10  $\mu\text{m}$  (Fig. (i, j) reprinted with permission by Taylor and Francis from Sheath and Whittick (1995); Fig. (f, h, k, l) redrawn from Skuja (1933))

**Diagnostic characters:** this genus can be distinguished from other genera in the Batrachospermales by a carposporophyte with zonately septated carposporangia forming chambers.

**Etymology:** the genus name is for one of the two locations in which this taxon has been collected; “genadendal” is Afrikaans for “Valley of Mercy.”

**Habitat:** this genus has been collected in the following environmental conditions (Sheath & Whittick 1995): water temperature 18 °C, pH 5.5, conductivity 21  $\mu\text{S cm}^{-1}$ , depth 10–20 cm, and 50% shading.

**Distribution:** this genus is currently known from Africa (Fig. 5.2).

**Key references:** Skuja (1933), Sheath et al. (1994b), Sheath and Whittick (1995).

*Genadendalia breutelii* (Rabenhorst) ML Vis and Necchi, **comb. nov.** (Fig. 5.3e–l)

**Basionym:** *Batrachospermum breutelii* Rabenhorst, Allg Deutsch Naturhist Zeit ser 2, 1:280 (1855).

**Type:** G 00261325, Herbarium AP De Candolle, JC Breutel, 1854 (Holotype); B 2816, S A16513 (Isotypes).

**Type locality:** South Africa: Genadendal, 34.041771° S, 19.562574° E.

**Description:** whorls 350–650  $\mu\text{m}$  in diameter; primary fascicles composed of 4–7 cells; spermatangia 7–9  $\mu\text{m}$  in diameter; carpogonial branches 3–6 cells, 25–50  $\mu\text{m}$  in length; carpogonia 60–95  $\mu\text{m}$  in length, 12–20  $\mu\text{m}$  in diameter; carposporophyte 185–400  $\mu\text{m}$  in diameter, 155–335  $\mu\text{m}$  in height; gonimoblast filaments with 1 cell; carposporangia 100–200  $\mu\text{m}$  in length and 50–90  $\mu\text{m}$  diameter, with 4–6 chambers.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Africa: South Africa (two locations in southern South Africa) (Fig. 5.2).

**Key references:** Skuja (1933), Sheath et al. (1994b), Sheath and Whittick (1995).

**Remarks:** gonimoblast propagules described by Sheath and Whittick (1995) are here interpreted as zonately septated carposporangia. This unique character among the Batrachospermales is the basis for distinguishing a new genus. The phylogenetic position of the genus within the Batrachospermales will only be possible when DNA sequence data become available.

*Lympha* JR Evans, IS Chapuis and ML Vis, Algae 32:175 (2017)

**Type species:** *Lympha mucosa* JR Evans, IS Chapuis, and ML Vis, Algae 32: 175 (2017).

**Description:** thalli monoecious; light green to dark blue-green or black; consistency mucilaginous; branching irregular; whorls reduced, dense, pear-shaped or obconical, compressed, indistinct in older parts; cortical filaments of the main axis well developed with cylindrical cells; primary fascicles with cells ranging from ellipsoidal to fusiform; secondary fascicles very abundant, covering the entire internode; spermatangia terminal or sub-terminal on primary and secondary fascicles or adjacent to the involucrel filaments; carpogonial branches straight, short, arising from the pericentral or proximal fascicle cells; involucrel filaments

short; carpogonia with unstalked, clavate, or elongate-lanceolate trichogynes; carposporophyte one per whorl, large, axial, sub-spherical to spherical, higher than whorls; gonimoblast filaments densely arranged, composed of cylindrical, ellipsoidal, or barrel-shaped cells; carposporangia obovoidal.

**Diagnostic characters:** this genus is similar to *Kumanoa*, *Paludicola*, *Torularia*, and *Virescentia* in having large, axial carposporophytes. It can be distinguished from *Virescentia* based on its reduced whorls. There are some *Kumanoa* species with reduced whorls, but *Kumanoa* has curved or curled carpogonial branches. *Paludicola* has species with reduced whorls, but the carposporophytes have two kinds of gonimoblast filaments (erect and prostrate). It is distinguished from *Torularia* by having non-audouinelloid fascicle cells and longer carpogonia ( $\geq 37$  vs.  $\leq 33.5$   $\mu\text{m}$ ).

**Habitat:** this species appears to be able to tolerate full sunlight to heavily shaded conditions with the thallus color reflecting the light conditions, light green (full sunlight), and blue green (shade). The only two known locations had water with pH 6.6–8.3 and conductivity 110–140  $\mu\text{S cm}^{-1}$ .

**Distribution:** this genus is currently known from North America (Fig. 5.2).

*Lympha mucosa* JR Evans, IS Chapuis, and ML Vis, *Algae* 32: 175 (2017) (Fig. 5.4a–c)

**Type:** NY 02137800 M. Vis, W. Chiasson, and O. Necchi Jr., 06.viii.2008 (Holotype), BHO A-176 (Isotype).

**Type locality:** the USA: Kentucky, Kinniconick River, 38.4966° N, 83.2572° W.

**Description:** whorls 154–223  $\mu\text{m}$  in diameter; primary fascicles composed of 4–7 cells; spermatangia 6.4–7.0  $\mu\text{m}$  in diameter; carpogonial branches 1–3 cells; carpogonia 37–49  $\mu\text{m}$  in length with trichogyne 9–13  $\mu\text{m}$  in diameter; carposporophyte 173–305  $\mu\text{m}$  in diameter and 151–247  $\mu\text{m}$  in height; gonimoblast filaments 2–3 cells; carposporangia 23–31  $\mu\text{m}$  in length and 14–20  $\mu\text{m}$  diameter.

**Representative sequences in GenBank:** KM593873 (COI-5P); KM593865 (*rbcL*).

**Distribution:** North America: the USA (Kentucky, Alabama) (Fig. 5.2).

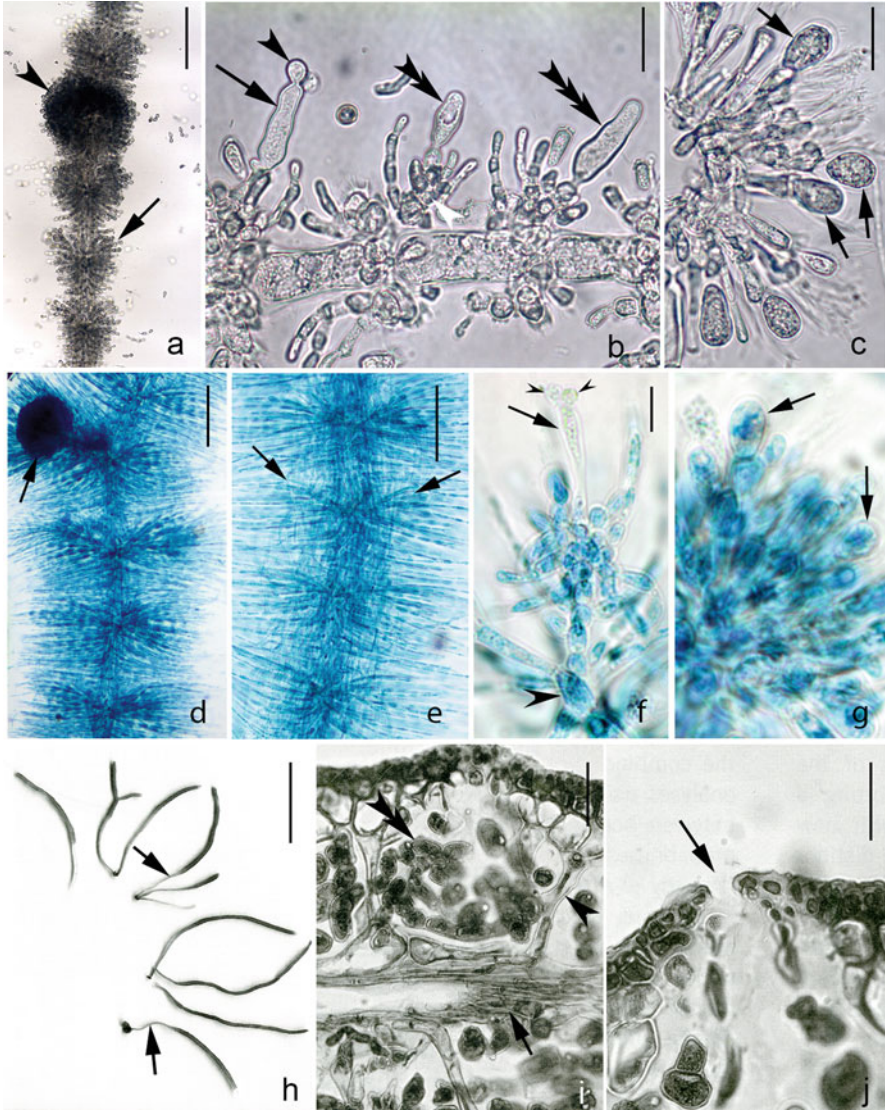
**Key reference:** Evans et al. (2017).

*Notohesperus* ML Vis, Entwisle, and Necchi **gen. nov.**

**Type species:** *Notohesperus serendipidus* (Entwisle and ML Vis) ML Vis, Entwisle, and Necchi.

**Description:** thalli monoecious; grass-green; branching irregular; whorls reduced, barrel-shaped, contiguous; cortication of the main thallus axis well developed with filaments of cylindrical cells detached from the main axis or loosely arranged; primary fascicles with cells ranging from ellipsoidal, fusiform to obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia terminal or sub-terminal on primary and secondary fascicles; carpogonial branches well differentiated from the fascicles, straight, short, arising from the pericentral or proximal fascicle cells, composed of barrel-shaped cells;





**Fig. 5.4** (a–c) *Lympha mucosa*: (a) reduced, pear-shaped whorls (arrow) with large axial carposporophyte (arrowhead) that is higher than the whorl; (b) three carpogonia along the branch: a mature carpogonium with elongate-lanceolate trichogyne (arrow) and attached spermatium (arrowhead), a developing carpogonium on a short-celled branch (white arrowhead) with a clavate trichogyne (double arrowhead), and an unfertilized carpogonium with a elongate-lanceolate trichogyne (triple arrowhead); (c) gonimoblast filaments with obovoid carposporangia (arrows); (d–g) *Notohesperus serendipidus*: (d) whorl with large pedunculate carposporophyte (arrow) (specimen TJE3364); (e) main axis with loose cortication (arrows) (specimen TJE3364); (f) carpogonium with narrow-clavate trichogyne (arrow) and spermatia (small arrowheads) on a multi-celled branch originating from pericentral cell (large arrowhead) (specimen TJE3352); (g) gonimoblast filaments with carposporangia (arrows) (specimen TJE3352). (h–j) *Petrohwa bernabei*: (h) thalli pseudoparenchymatous tubular morphology with distinct stalk (arrows); (i) longitudinal section through mature thallus showing cortication around main axis (arrow), ray cells (arrowhead) and abundant

involucral filaments short, composed of 2–6 barrel-shaped to cylindrical cells; carpogonia with stalked, narrow-clavate to clavate trichogynes; carposporophytes pedunculate, sometimes protruding from the whorl, spherical, one per whorl; gonimoblast filaments densely arranged; carposporangia ellipsoidal or obovoidal.

**Diagnostic characters:** this genus has pedunculate carposporophytes similar to *Batrachospermum*, *Sheathia*, *Montagnia*, and *Visia*, and loose cortication of the main axis like *Paludicola*. Using the combination of these two characters, it can be distinguished from all other genera in the Batrachospermales.

**Etymology:** the genus name means “South West” in Greek. This taxon is thus far known only from two locations in Southwest Tasmania, Australia, within the South West Wilderness area.

**Habitat:** Attached to rocks, roots or in sand, in slow-flowing humic streams through button grass moorland.

**Distribution:** this genus is currently known from Australasia (Fig. 5.2).

*Notohesperus serendipidus* (Entwisle and ML Vis) ML Vis, Entwisle, and Necchi **comb. nov.** (Fig. 5.4d–g)

**Basionym:** *Batrachospermum serendipidum* Entwisle and ML Vis, J Phycol 52: 386 (2016).

**Type:** NSW 747863, T. J. Entwisle 3364, 05.vii.2007 (Holotype).

**Type locality:** Australia: Tasmania, Southwest National Park, tributary of Red Tape Creek, 43.0181° S, 146.3714° E.

**Description:** whorls 400–700 µm in diameter; primary fascicles composed of 5–7 cells; spermatangia ~7 µm in diameter; carpogonial branches 5–8 cells, 37–59 µm in length; carpogonia 27–35 µm in length with trichogyne 5–7 µm in diameter; carposporophyte 140–200 µm in diameter; gonimoblast filaments 2–5 cylindrical or barrel-shaped cells; carposporangia 12–15 µm in length and 6–10 µm diameter.

**Representative sequences in GenBank:** KT802753 (COI-5P); KT802837 (*rbcL*).

**Distribution:** Australasia: Australia (southwest Tasmania) (Fig. 5.2).

**Key reference:** Entwisle et al. (2016).

*Petrohua* GW Saunders, Phycol Res 55: 111 (2007)

**Type species:** *Petrohua bernabei* GW Saunders, Phycol Res 55:111 (2007).

**Description:** thalli monoecious; cartilaginous, pseudoparenchymatous tubular; stalked with weak division into node and internode regions; rarely branched; small photosynthetic outer cortex cells and larger non-photosynthetic inner cells; internal construction consisting of uniaxial central filament surrounded by abundant cortical filaments; spermatangia in circular papillae at nodes; putative

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**Fig. 5.4** (continued) carposporangia (*double arrowhead*); (**j**) opening (ostiole-like) in the thallus (*arrow*) through which carpospores may be released. *Scale bars:* (**h**) = 1 cm; (**a**) = 150 µm; (**d, e**) = 100 µm; (**f, g**) = 50 µm; (**e**) = 30 µm; (**i**) = 25 µm; (**b**) = 20 µm; (**j**) = 15 µm (Fig. (h–j) reprinted with permission by Wiley from Vis et al. (2007))

carpogonium with clavate trichogyne and developing from a cluster of cells; carposporangia in chains and putatively released through ostiole-like openings in the outer cortex.

**Diagnostic characters:** among the tubular genera (*Lemanea*, *Paralemanea*, *Petrohua*, and *Psilosiphon*), this genus is distinguished from the others by the combination of spermatangia arranged in circular papillae at the nodes, cortication around the main axis, and carposporangia released through openings in the outer cortex; in addition, *Petrohua* is similar to *Lemanea* and *Paralemanea* in having outer cortical cells decreasing in size towards periphery and distinct from *Psilosiphon* that has outer and inner cortical cells similar in size.

**Habitat:** waterfall area with high current velocity.

**Distribution:** this genus is currently known from South America (Fig. 5.2).

*Petrohua bernabei* GW Saunders, Phycol Res 55:111 (2007) (Fig. 5.4h–j)

**Type:** UNB GWS000521, GW Saunders, 16.xii.1989 (Holotype).

**Type locality:** Chile: Saltos del Rio Petrohue, 41.3667° S, 72.3167° W.

**Description:** thalli olive-green, rarely branched, weakly nodose, 1–7 cm length, 300–600 µm nodal diameter; internodal diameter and length not measured; spermatangial papillae circular; putative carpogonium with clavate trichogyne, 16 µm in length, 5 µm in diameter; carposporangia in chains, obovoidal to ellipsoidal, 17.8–21.1 µm in length and 7.9–11.2 µm diameter; “Chantransia” not described.

**Representative sequences in GenBank:** KM055336 (COI-5P); AY960690 (*rbcL*).

**Distribution:** South America: Chile, known from the type locality only (Fig. 5.2).

**Key reference:** Vis et al. (2007).

*Psilosiphon* Entwisle, Phycologia 28:470 (1989b)

**Type species:** *Psilosiphon scoparius* Entwisle, Phycologia 28:470 (1989b).

**Description:** thalli cartilaginous, pseudoparenchymatous, tubular; olive-green; narrow at the base, gradually becoming wide (unstaked) with no division into node and internode regions; unbranched, but sometimes with branching near base. Putative spermatangia, no carpogonia observed. Cortex composed of ellipsoidal to obovoidal photosynthetic cells of uniform size in distinct outward radiating rows or filaments; dense medullary filaments composed of cylindrical cells, colorless, in between the outer cortex and the uniaxial central filament. Reproduction by putative monosporangia formed in chains from the cortical filaments on the outside of the thallus or adventitious plantlets.

**Diagnostic characters:** this genus can be distinguished from the other three tubular genera (*Lemanea*, *Paralemanea*, and *Petrohua*) by the following characteristics: cortex composed cells in outward radiating rows or filaments as well as densely interwoven medullary filaments such that the thallus is not hollow, monospores formed in chains on outer part of the thallus and reproduction by adventitious plantlets from the cortex.



**Habitat:** humic, oligotrophic streams flowing over sandstone; a single stream, one-time measures of pH <6, water temperature 16 °C, and conductivity 80  $\mu\text{S cm}^{-1}$ .

**Distribution:** this genus is currently known from Australasia (Fig. 5.2).

**Key references:** Entwisle (1989b), Sheath et al. (1996), Entwisle et al. (2000).

*Psilosiphon scoparius* Entwisle, Phycologia 28: 470 (1989b) (as “scoparium”) (Fig. 5.5a–d)

**Type:** MEL2027162 T.J. Entwisle and R.A. Anderson, 11.xi.1988 (Holotype), MEL695335, MEL 2355265A (Isotypes).

**Type locality:** Australia: New South Wales, Barren Grounds Nature Reserve, Lyrebird Creek.

**Description:** thalli with simple branching near the base; simple tube and not nodulose, 14–33(–60) mm in length, 500–1500  $\mu\text{m}$  in diameter; putative spermatangia of similar size to monosporangia; monosporangia in chains on the outside of thallus, spherical, obovoidal, 15.6–20.3  $\mu\text{m}$  in length, 13.9–18.8  $\mu\text{m}$  in diameter.

**Representative sequences in GenBank:** KT8002770, KU672392 (COI-5P); AF029155, AF149028, KT802770 (*rbcL*).

**Distribution:** Australasia: Australia (New South Wales and Tasmania) and New Zealand. (Fig. 5.2).

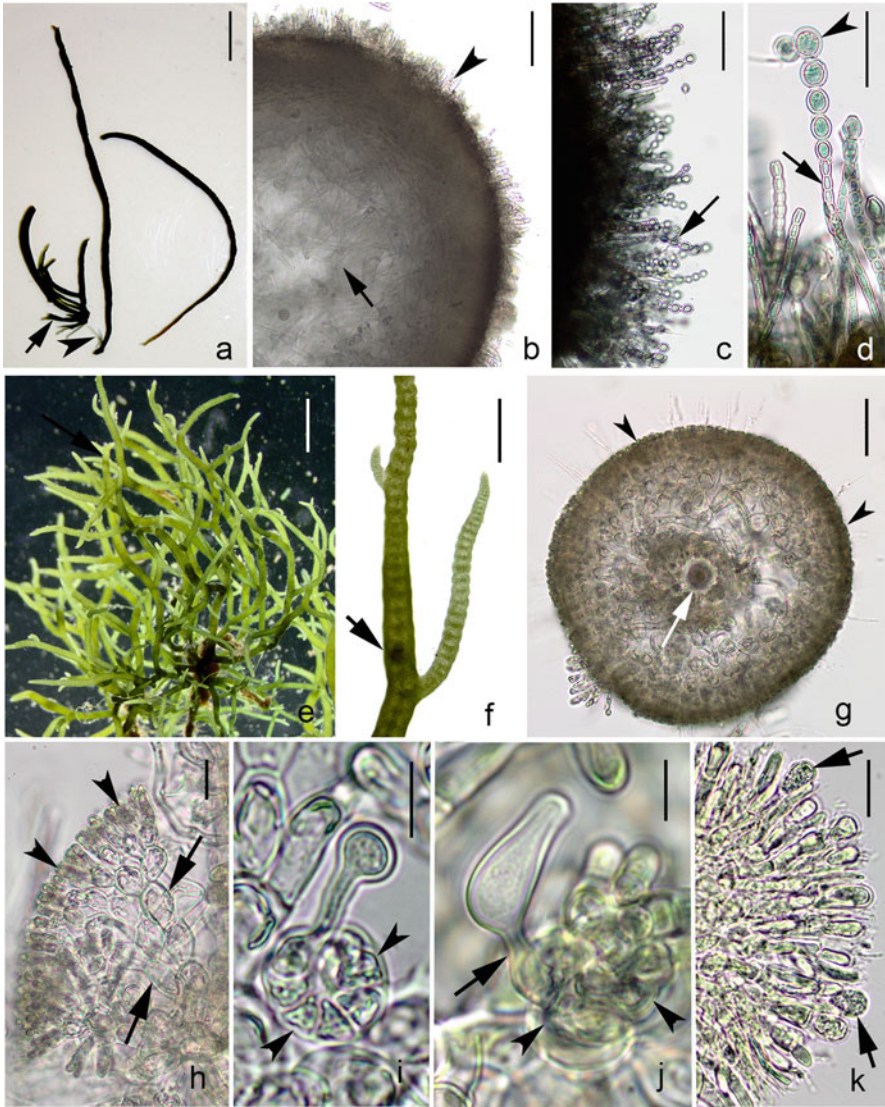
**Key references:** Entwisle (1989b), Sheath et al. (1996), Entwisle et al. (2000).

**Remarks:** three genetic races, New Zealand, Tasmania, New South Wales were recognized in Entwisle et al. (2000) based on divergent *rbcL* sequence data among them (4.8–7.7%). The high sequence variation may indicate cryptic species with little morphological differentiation. The holotype specimen in the protologue (MELU TJE1565) was transferred to MEL2027162; although labeled isotype on JSTOR, it is the holotype.

*Tuomeya* Harvey, Smithsonian C Know 10:64 (1858)

**Type species:** *Tuomeya americana* (Kütz) Papenfuss, Taxon 7:107 (1958).

**Description:** thalli monoecious, dark blue-green, cartilaginous, pseudoparenchymatous; branching irregular; whorls dense, barrel-shaped, compressed and indistinct, cortication of the main axis well developed with filaments of ellipsoidal, obovoidal, and spherical cells; primary fascicles with proximal cells spherical, inflated, clear in appearance and distal cells small, dense and photosynthetic; secondary fascicles sparse; spermatangia on primary or secondary fascicles; carpogonial branches composed of disc-shaped cells, curved or curled, developing from the periaxial or proximal cells of primary fascicles; involucrel filaments lacking or 1-celled; carpogonia with stalked, a-symmetrical, obliquely bent and sometimes almost perpendicular, with stalked or unstalked, club-shaped, cylindrical inflated, or elongate-conical trichogynes; carposporophytes small, axial, obovoidal, or spherical, developing within the pseudoparenchymatous thallus and



**Fig. 5.5** (a–d) *Psilosiphon scoparius*: (a) thallus habit showing basal branches (arrow) and small plantlets (arrowhead); (b) thallus cross section with medulla composed of densely interwoven filaments (arrow) and outer cortex with rows of cells (arrowhead); (c) cortex composed of cells in rows (arrow); (d) cortex filaments having vegetative cells (arrow) near base and chains of putative monosporangia near the tips (arrow). (e–k) *Tuomeya americana*: (e) habit of thallus in darkfield showing the pseudoparenchymatous construction with whorls barely discernable; (f) whorls only evident from banding pattern with dense carposporophyte (arrow) visible within the thallus structure; (g) cross section of thallus showing the axial cell of the main axis (arrow) and the tip cells of the fascicles densely arranged forming the pseudoparenchymatous construction (arrowheads); (h) fascicles composed of large, ellipsoidal, obovoidal or spherical, clear cells (arrows) and smaller, densely arranged photosynthetic cells at the tips (arrowheads); (i) developing carpogonium with stalked trichogyne (arrow) on a curled branch (arrowheads); (j) carpogonium with an unstalked oblique, asymmetrical trichogyne (arrow) on a curved branch (arrowheads); (k) gonimoblast filaments with obovoidal carposporangia (arrows). Scale bars: (a) = 10 mm; (e) = 1 mm; (f) = 500  $\mu$ m; (b, c) = 100  $\mu$ m; (d, g) = 50  $\mu$ m; (h) = 25  $\mu$ m; (k) = 15  $\mu$ m; (i, j) = 10  $\mu$ m

appearing as darken patches; gonimoblast filaments densely arranged, composed of barrel-shaped cells; carposporangia obovoidal.

**Diagnostic characters:** cartilaginous, pseudoparenchymatous *Batrachospermum*-like gametophyte, in which the fascicles of the whorls are compressed together to be pseudoparenchymatous. This taxon can be easily differentiated from *Lemanea*, *Paralemanea*, *Petrohua*, and *Psilosiphon* because these pseudoparenchymatous genera form tube-like thalli whereas *Tuomeya* is highly branched like the other *Batrachospermum*-like species. *Tuomeya* is most like *Nothocladus* that also has been noted to have species with pseudoparenchymatous construction; *Tuomeya* has a cross section that clearly shows the fascicle cells inflated, obovoidal, and densely packed filling the space between the main axis and outer cells, whereas *Nothocladus* has slender, ellipsoidal fascicle cells and more open spaces between the main axis and outer cells.

**Habitat:** streams with a wide range in temperature 5–26 °C, current velocity 16–125 cm s<sup>-1</sup>, pH 4.7–7.6, and conductivity 10–124 μS cm<sup>-1</sup> and gametophytes present from fall to early summer according to Sheath and Vis (2015).

**Distribution:** this genus is currently known from North America (Fig. 5.2).

**Key references:** Setchell (1890), Skuja (1944), Papenfuss (1958), Kaczmarczyk et al. (1992), Sheath and Vis (2015).

**Remarks:** there are dubious reports outside of North America (Asia, Europe, and South Africa) of this genus that need to be verified using morphology and DNA sequence data and were not considered here. Other *Batrachospermum*-like taxa can superficially resemble *Tuomeya* when specimens have been grazed or are old, particularly some species of *Paludicola* and *Kumanoa*.

*Tuomeya americana* (Kütz) Papenfuss, Taxon 7:107 (1958) (Fig. 5.5a–g)

**Basionym:** *Baileya americana* Kütz, Tabulae Phycologicae:35 (1857).

**Type:** L4086532, J. Bailey, no date (Lectotype), TCD0011953 (Isotype).

**Type locality:** the USA: Virginia, near Fredericksburg 38.303184° N, 77.460540° W (estimated).

**Description:** thalli monoecious, dark blue-green, cartilaginous, pseudoparenchymatous, whorls 177–674 μm in diameter; primary fascicles composed of 5–7 cells; spermatangia 3.5–6 μm in diameter; carpogonial branches 6–9 cells; carpogonia 25–55.8 μm in length with trichogyne 7.1–11.4 μm in diameter; carposporophyte 110–150 μm in diameter; gonimoblast filaments 2–4(–5) cells; carposporangia 10.2–16 μm in length and 7.1–10 μm diameter.

**Representative sequences in GenBank:** KM055330, MF940788 (COI-5P); MG321573, MG321580 (*rbcL*).

**Distribution:** North America: Canada (eastern), the USA (northeast and southeast) (Fig. 5.2).

**Remarks:** Kaczmarczyk et al. (1992) reported a wide range in carposporangia size (3.4–11.7 × 5.1–16.1 μm), which seems unusually broad; in the description provided here, the ranges are from in material observed and photographed for this book and Skuja (1944); likewise, since there were no measurements for

carposporophytes, these are from new material; for all other measurements, data from Kaczmarczyk et al. (1992), Skuja (1944), and new material were utilized.

## Genera with Two or Three Species: *Montagnia*, *Nocturama* and *Volatus*

*Montagnia* Necchi, ML Vis, and AS Garcia, Phycologia 58:587 (2019c)

**Synonym:** *Batrachospermum* section *Macrospora* (Kumano) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:713 (2009); *Batrachospermum* section *Aristata* subsection *Macrospora* Kumano, Jap J Phycol 41:263 (1993).

**Type species:** *M. macrospora* (Montagne) Necchi, ML Vis, and AS Garcia, Phycologia 58:587 (2019c).

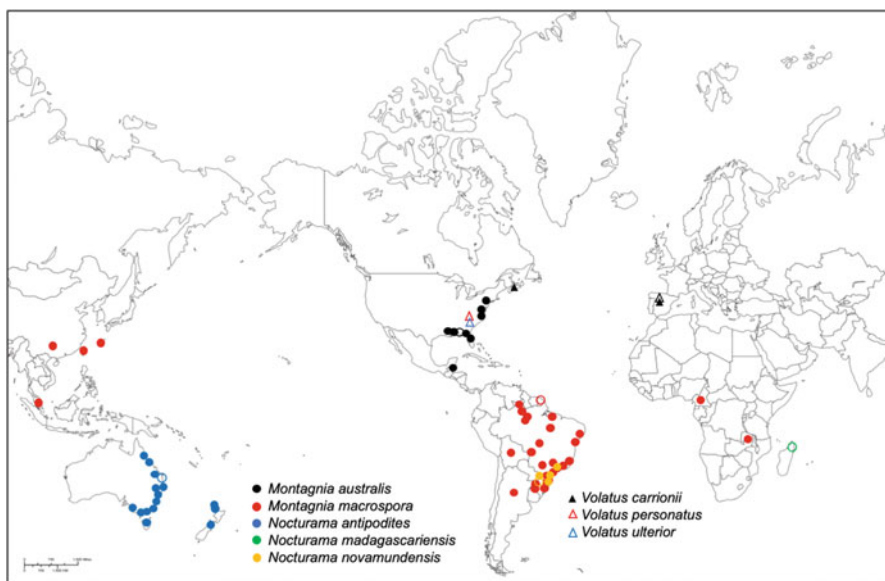
**Description:** thalli monoecious, dioecious, or polyecious; bluish or greenish-blue, consistency mucilaginous; branching irregular; whorls well developed, contiguous or separated, barrel-shaped, obconical or pear-shaped or spherical; cortication of the main thallus axis well developed with filaments of cylindrical cells; primary fascicles straight, formed by cylindrical, ellipsoidal, obovoidal, or spherical cells; secondary fascicles abundant and covering half to the entire internode; monosporangia obovoidal or pear-shaped, terminal on primary or secondary fascicles; spermatangia spherical or obovoidal, terminal or sub-terminal on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, straight, long, developing from the periaxial or proximal cells of primary fascicles, on carpogonial branches rarely from cortical filaments, composed of short-cylindrical or barrel-shaped cells; involucrel filaments composed of 3–10 ellipsoidal or fusiform proximal cells and usually 1–2 sub-spherical or ellipsoidal upper distal cells forming a rosette around the carpogonia; carpogonia sessile or stalked with clavate or pear-shaped trichogynes; fertilized carpogonia and subtending cells of carpogonial branches with enlarged pit connections (>3 µm wide); carposporophytes pedunculate, spherical or sub-spherical, contained within the whorls, small; gonimoblast filaments densely arranged, composed of 1–5 cylindrical or barrel-shaped cells; carposporangia large, obovoidal, or pear-shaped.

**Diagnostic characters:** *Montagnia* most closely resembles members of the genus *Visia* in having well-developed whorls, long carpogonial branches that are well differentiated from the fascicles, short carpogonia, pedunculate carposporophytes, gonimoblast filaments of one type, densely arranged and arising radially from the fertilized carpogonia. *Montagnia* can be distinguished from *Visia* by the presence of upper distal cells of involucrel filaments forming a rosette around the carpogonia, cells of post-fertilized carpogonial branches with enlarged pit connections and large carposporangia.

**Habitat:** the two species of *Montagnia* occur typically in rivers or streams with black water (yellow to dark brown color) in partly shaded or shaded, less often in open habitats, sandy bottom and usually attached to sticks, fallen tree logs or epiphytic on macrophytes. *Montagnia macrospora* has been observed in the following environmental conditions (Necchi et al. 1999; unpublished data): high water temperature 20–28.8 °C ( $24.8 \pm 3.4$  °C), low conductivity (2–79,  $16 \pm 21$   $\mu\text{S cm}^{-1}$ ), low pH (4.3–6.7,  $5.3 \pm 1$ ), moderate to high saturation of dissolved oxygen (55–83,  $64 \pm 10\%$ ), and moderate current velocity (3–60,  $38 \pm 7$   $\text{cm s}^{-1}$ ). *Montagnia australis* has been reported at similar conditions (Sheath et al. 1994b; Redmond et al. 2019): high water temperature 20–27 °C ( $23.4 \pm 2$  °C), low conductivity (2–37,  $18 \pm 9$   $\mu\text{S cm}^{-1}$ ), and low pH (5.2–6.1,  $5.7 \pm 0.3$ ).

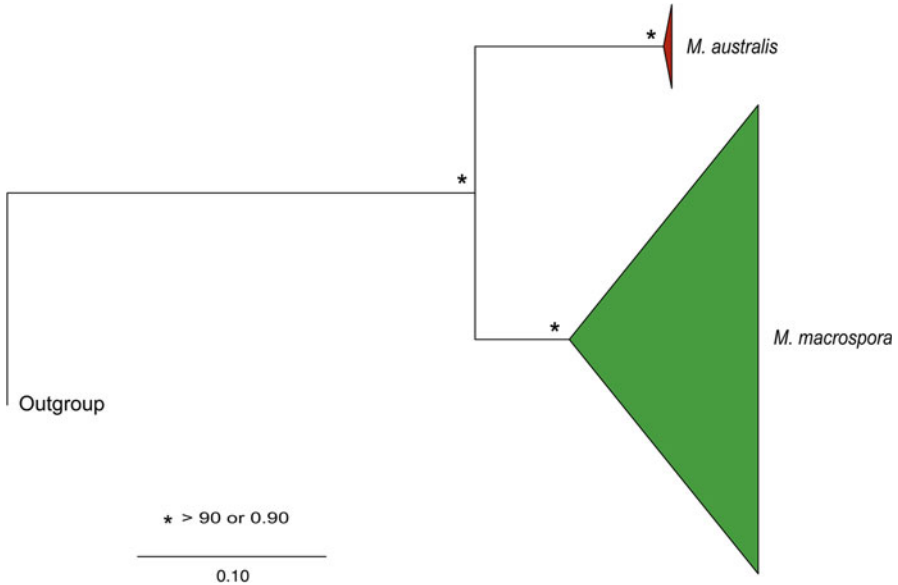
**Distribution:** *Montagnia* has been reported mostly in tropical and sub-tropical, less often in temperate regions. *Montagnia macrospora* is pan-tropical with few records in Africa and Asia and widespread in South America, whereas *M. australis* occurs in North America, from New Jersey in the North to Belize in the South, but primarily recorded from the coastal plain in the southeastern USA (Fig. 5.6).

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences for the two species showed the genus with full support, as well as the clades representing the two species (Fig. 5.7). The genetic diversity reported in *M. macrospora* is the highest among the members of the Batrachospermales for *rbcL* and COI-5P, whereas is much lower in *M. australis* (Necchi et al. 2019c). Phylogeographic



**Fig. 5.6** World map showing the distribution of the species of *Montagnia*, *Nocturama*, and *Volatus*. Open symbols represent type localities





**Fig. 5.7** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships between the two species of *Montagnia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

data indicate a high variation among haplotypes for *cox2-3* of *M. macrospora* from South America and suggest that the Amazonian region served as a center of diversity (Vis et al. 2008).

***Montagnia australis*** (Collins) Necchi and ML Vis, *Phycologia* 58:588 (2019c) (Fig. 5.8a–d)

**Basionym:** *Batrachospermum australe* Collins, *Rhodora* 8:110 (1906).

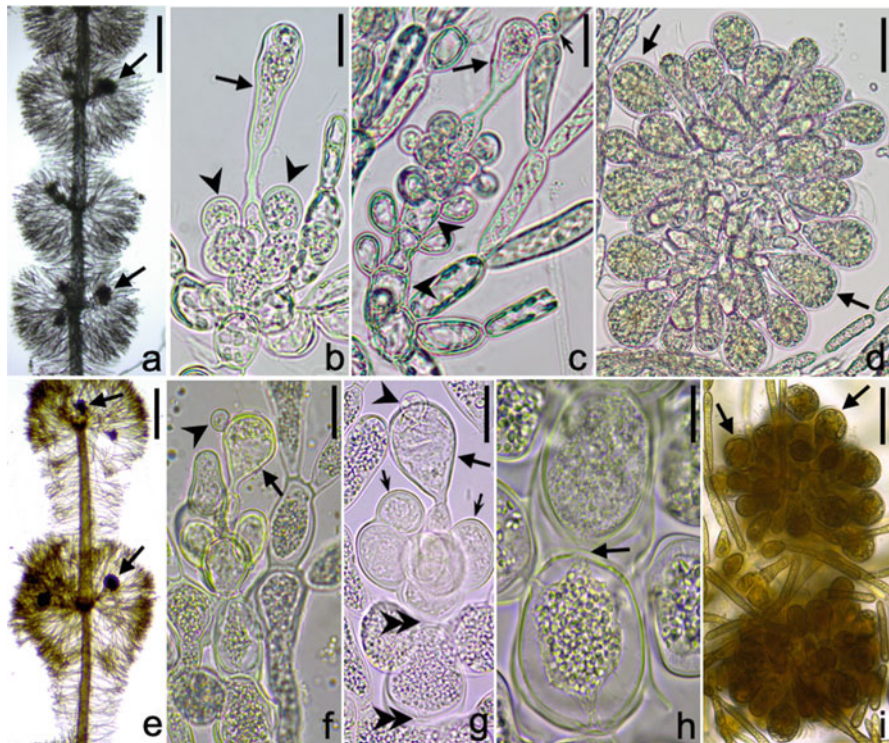
**Type:** MICH 642701, DA Saunders (Lectotype, Sheath et al. 1994b).

**Type locality:** the USA, Alabama, Mobile Bay, Fly Creek, 30.557593° N, –87.879571° W.

**Description:** whorls 390–1160 μm in diameter; primary fascicles with (4–)6–8(–10) cells; spermatangia 4.5–10 μm in diameter; carpogonial branches with 4–13 cells, (47–)60–100(–156) μm in length; carpogonia 37–72 μm in length, 10–17.5 μm in diameter; carposporophytes 1–3(–5) per whorl, 67–211 μm in diameter; carposporangia 24–42 μm in length, 16–30 μm in diameter.

**Diagnostic characters:** this species tends to have lower number of cells in primary fascicles (usually ≤8 cells), longer carpogonia (up to 70 μm in length), and smaller carposporangia (≤42 μm in length, (≤30 μm in diameter) than *M. macrospora* but there is a considerable overlap: up to 12 cells, carpogonia up to 50 μm in length and carposporangia up to 66 μm in length and 45 μm in diameter. These species can only be unequivocally separated based on DNA





**Fig. 5.8** (a–d) *Montagnia australis*: (a) barrel-shaped whorls with stalked carposporophytes (arrows); (b) mature carpogonium with clavate trichogyne (arrow) and distal cells of involucrel filaments forming a rosette around the carpogonium (arrowheads); (c) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (small arrow) and carpogonial branch cells (arrowheads); (d) carposporophyte with large carposporangia (arrows); (e–i) *Montagnia macrospora*: (e) obconical whorls with stalked carposporophytes (arrows); (f) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (g) fertilized carpogonium with clavate trichogyne (arrow), attached spermatium (arrowhead), distal cells of involucrel filaments forming a rosette around the carpogonium (small arrows), and carpogonial branch cells with enlarged pit connections (double arrowheads); (h) post-fertilization cells of carpogonial branch with enlarged pit connection (arrow); (i) two carposporophytes with large carposporangia (arrows). Scale bars: (a, e) = 200 µm; (i) = 50 µm; (d) = 25 µm; (b, c, f, g) = 10 µm; (h) = 5 µm

sequence data, but geographic distribution is an additional criterion since *M. australis* occurs only in North America, whereas *M. macrospora* is pantropical (Africa, Asia, and South America).

**Representative sequences in GenBank:** EU636755, EU636759, KT802766 (COI-5P); AF029145, EU106052, EU106055 (*rbcl*).

**Distribution:** North America: Belize, the USA (coastal plain, southeastern) (Fig. 5.6).

**Key references:** Sheath et al. (1994b), Necchi et al. (2019c), Redmond et al. (2019).

***Montagnia macrospora*** (Montagne) Necchi, ML Vis, and AS Garcia, *Phycologia* 58:587 (2019c) (Fig. 5.8e–i)

**Basionym:** *Batrachospermum macrosporum* Montagne, *Ann. Sci. Nat., Botanique* 14:293 (1850).

**Type:** PC0452180, FMR Leprieur 1105 (Holotype); PC0473630-PC0473633 (Isotypes).

**Type locality:** French Guiana, Orapa and Comté rivers, 4.480787° S, 52.525817° W (estimated).

**Description:** whorls 500–2500 µm in diameter; primary fascicles with 5–10(–12) cells; monosporangia 40–56.5 µm in length, 23–30.5 µm in diameter; spermatangia 5–11 µm in diameter; carpogonial branches with 4–12(–16) cells, (40–)60–200(–260) µm in length; carpogonia 28–50 µm in length, 12–18 µm in diameter; carposporophytes 1–3(–4) per whorl, 80–220(–285) µm in diameter; carposporangia 30–66 µm in length, 20–45 µm in diameter.

**Diagnostic characters:** this species is only unequivocally distinguished from *M. australis* based on DNA sequence data, but geographic distribution is helpful because it does not occur in North America to which *M. australis* is restricted.

**Representative sequences in GenBank:** EU636750, MK532360, MK304453 (COI-5P); AY423415, MK304442, MK304441 (*rbcL*).

**Distribution:** Africa: Cameroon, Nigeria, Zambia; Asia: China, Japan, Taiwan; South America: Argentina, Bolivia, Brazil, French Guiana (Fig. 5.6).

**Key references:** Necchi (1990), Necchi et al. (2019c).

***Nocturama*** Entwisle and ML Vis, *J Phycol* 52:388 (2016)

**Synonym:** *Ahidranoa* E Fischer, D Killmann, and D Quandt, *Pl Fung Syst* 65: 159 (2020).

**Type species:** *N. antipodites* (Entwisle) Entwisle and ML Vis, *J Phycol* 52: 389 (2016).

**Description:** thalli monoecious or dioecious, brownish to brownish-red, less often dark greyish, consistency mucilaginous; branching irregular; whorls well developed, separated or obconic, spherical, barrel-shaped or obconical; cortication of the main thallus axis well developed with filaments of cylindrical cells; primary fascicles curved or straight, formed by cylindrical, ellipsoidal, obovoidal, or audouinelloid cells; secondary fascicles absent and few, only near the nodes or abundant and covering one-third to half of the internode; spermatangia spherical or obovoidal, terminal on primary, rarely on secondary fascicles; carpogonial branches well differentiated from the fascicles, little differentiated in one species, straight, short or long, developing from the periaxial or proximal cells of primary fascicles, composed of barrel-shaped or cylindrical cells; involucrel filaments composed of short-cylindrical or barrel-shaped cells, distal ones short (1–2 cells) and distal ones long (3–5 cells); carpogonia sessile with clavate, pear- or bottle-shaped trichogynes; carposporophytes pedunculate or short-pedunculate, spherical, in the inner or outer part of the whorls, 1–2 per whorl, small; gonimoblast filaments densely arranged, composed of short-cylindrical or barrel-shaped cells; carposporangia small, obovoidal.

**Diagnostic characters:** *Nocturama* most closely resembles members of the genera *Batrachospermum* and *Sheathia* (homocorticate species) in having relatively long carpogonial branches, short trichogynes, and pedunculate carposporophytes, as well as in lacking secondary fascicles (except in one species). It can be distinguished from both genera by the presence of only one or two larger carposporophytes per whorl that are large in comparison to the whorl and with shorter peduncles. In contrast, members of *Batrachospermum* and *Sheathia* typically have more numerous carposporophytes (two to six, exceptionally up to ten, per whorl) that are much smaller than the whorls and usually with longer peduncles. In addition to morphological characters, geography may be useful as no *Batrachospermum* species and only *Sheathia murphyi* and *S. transpacific* overlap the current known southern hemisphere distribution of *Nocturama*.

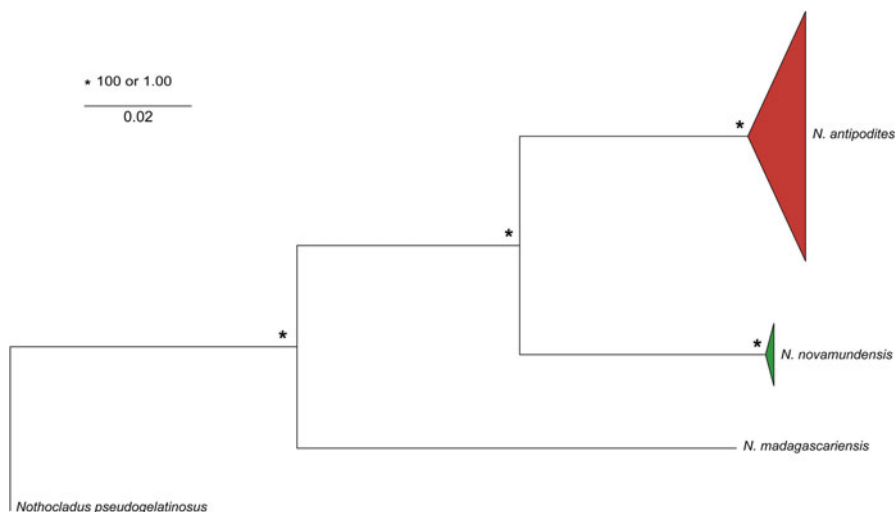
**Habitat:** species of *Nocturama* occur typically in shaded segments of streams or rivers or in shaded microhabitats in sunny sites. In terms of environmental data, *N. novamundensis* was reported in water temperature  $16.6 \pm 3.4$  °C, conductivity  $31 \pm 8$   $\mu\text{S cm}^{-1}$ , pH  $6.8 \pm 0.5$ , dissolved oxygen  $5.4 \pm 1.2$   $\text{mg l}^{-1}$ , current velocity  $55 \pm 25$   $\text{cm s}^{-1}$  (Necchi et al. 2016), whereas *N. antipodites* has a single record at 11 °C, pH 5.7, and conductivity  $130$   $\mu\text{S cm}^{-1}$  (Entwisle and Kraft 1984).

**Distribution:** this genus has been reported to date from southern hemisphere on three distinct continents: Africa, Australasia, and South America (Fig. 5.6). Two species are relatively widespread, *N. antipodites* (in eastern Australia and New Zealand) and *N. novamundensis* in southern and southeastern Brazil, whereas *N. madagascariensis* has been reported so far only in two localities in Madagascar.

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences for the three species showed the genus with full support, as well as the clades representing the species (Fig. 5.9). *Nocturama madagascariensis* was proposed as a new genus (*Ahidranoa*) by Fischer et al. (2020) but the phylogenetic relationship clearly indicates that it can be included in the genus. There is substantial genetic diversity within the genus, as well as within the most widespread species *N. antipodites*.

Key to the species of the genus *Nocturama*

1a	Secondary fascicles abundant, covering one-third to half of the internode length; carpogonia wide (13–15 $\mu\text{m}$ in diameter) with pear- or bottle-shaped trichogyne	<i>N. madagascariensis</i>
1b	Secondary fascicles absent or few and only near the node; carpogonia narrow (4–8 $\mu\text{m}$ in diameter) with clavate trichogyne	2
2a	Primary fascicles straight, with audouinelloid (exclusively cylindrical) cells; known distribution in Australia and New Zealand	<i>N. antipodites</i>
2b	Primary fascicles curved, with cylindrical, ellipsoidal, or obovoidal cells; known distribution in South America	<i>N. novamundensis</i>



**Fig. 5.9** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Nocturama*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

*Nocturama antipodites* (Entwisle) Entwisle and ML Vis, *J Phycol* 52:389 (2016) (Fig. 5.10a–d)

**Basionym:** *Batrachospermum antipodites* Entwisle, *Muelleria* 8:291 (1995).

**Type:** MEL 2020014, TJ Entwisle 2236, 06.ix.1993 (Holotype); BRI (Isotype).

**Type locality:** Australia, Queensland, Kondalilla National Park, Kondalilla Falls, Skene Creek, 26.666667° S, 152.866667° E.

**Description:** thalli monoecious; whorls contiguous or separated, spherical or barrel-shaped, 330–800 µm in diameter; primary fascicles straight, with 8–13 audouinelloid, cylindrical cells; secondary fascicles absent or few and near the node; spermatangia 5–8 µm; carpogonial branches straight, composed of 4–9 barrel-shaped or short-cylindrical cells, developing from proximal cells of primary fascicles, 30–55 µm in length; carpogonia with sessile and clavate trichogynes, 19–39 µm in length, 4–8 µm in diameter; carposporophytes 1, rarely 2, per whorl, 70–200 µm in diameter; gonimoblast filaments with 4–5 barrel-shaped or short-cylindrical cells; carposporangia 10–18 µm in length, 6–12 µm in diameter.

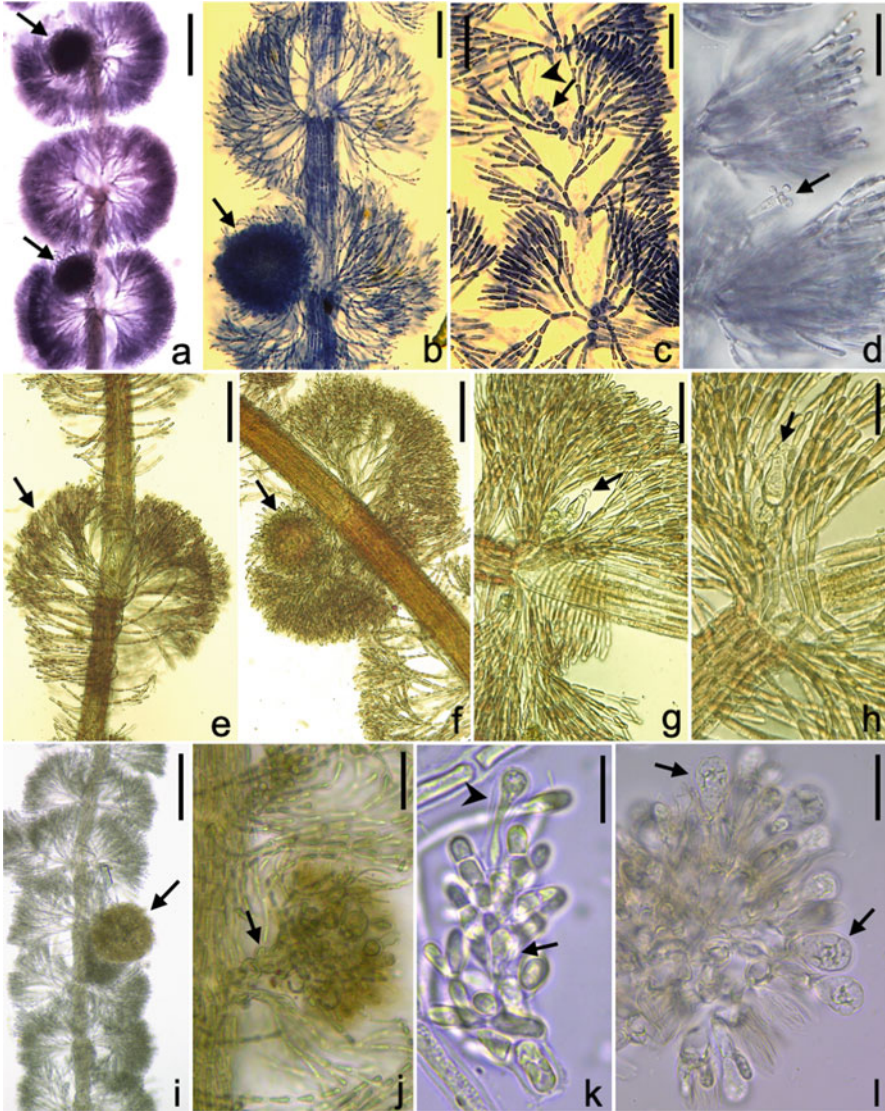
**Diagnostic characters:** this species is distinct from the others of the genus by the presence of primary fascicles with audouinelloid (exclusively cylindrical) cells, lack of secondary fascicles, narrow carpogonia (4–8 µm in diameter) with clavate trichogyne and distribution restricted to Australia and New Zealand.

**Representative sequences in GenBank:** KT894754, KT894754 (COI-5P); AY423420, KT802838 (*rbcL*).

**Distribution:** Australasia: Australia and New Zealand (Fig. 5.6).

**Key references:** Entwisle (1995), Entwisle and Foard (2007), Entwisle et al. (2016).





**Fig. 5.10** (a–d) *Nocturama antipodites*: (a) spherical whorls with short pedunculate carposporophytes (arrows); (b) whorls with primary fascicles and a short pedunculate carposporophyte (arrow); (c) whorls with carpogonial branch (arrow) and carpogonium with clavate trichogyne (arrowhead); (d) carpogonium emerging from a whorl with clavate trichogyne and attached spermatia (arrow); (e–h) *Nocturama madagascariensis*: (e) obconical whorl with curved primary fascicles (arrow); (f) whorl with a short pedunculate carposporophyte (arrow); (g, h) whorls with mature carpogonia, bottle-shaped trichogynes and attached spermatia (arrows); (i–l) *Nocturama novamundensis*: (i) barrel-shaped whorls with a short pedunculate carposporophyte (arrow); (j) developing carposporophyte with a peduncle (arrow); (k) carpogonial branch (arrow) with mature carpogonium and clavate trichogyne (arrowhead); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (a, i) = 200 µm; (b, e) = 100 µm; (c, g, j) = 50 µm; (d, h) = 25 µm; (k, l) = 10 µm (Image authors: Fig. (a–d) T Entwistle; Fig. (e–h) E Fischer)

*Nocturama madagascariensis* (E Fischer, D Killmann, and D Quandt) Necchi and ML Vis, **comb. nov.** (Fig. 5.10e–h)

**Basionym:** *Ahidranoa madagascariensis* E Fischer, D Killmann, and D Quandt, *Pl Fung Syst* 65:159 (2020).

**Type:** TAN, E Fischer 799/17 (AC 076), 30.ix.2017 (Holotype); KOBL (Isotype).

**Type locality:** Madagascar, Antsiranana, Parc National de Masoala, River Ambanizana, 15.449967° S, 50.008181° E.

**Description:** thalli monoecious; whorls contiguous or separated, obconical, or barrel-shaped, 150–500 µm in diameter; primary fascicles curved, with 9–13 cylindrical, ellipsoidal, or obovoidal cells; secondary fascicles abundant, covering one-third to half of the internode; spermatangia 4.5–6 µm in diameter; carpogonial branches composed of 11–13 barrel-shaped or short-cylindrical cells, developing from periaxial or proximal cells of primary fascicles, 18–35 µm in length; carpogonia with sessile and pear-shaped or bottle-shaped trichogynes, 30–45 µm in length, 13–15 µm in diameter; carposporophytes 1 per whorl, 58–120 µm in diameter; carposporangia 7.5–9 µm in length, 6–7.5 µm in diameter.

**Diagnostic characters:** this species is distinct from the others of the genus by the presence of non-audouinelloid primary fascicles with cells variable in shape (cylindrical, ellipsoidal, or obovoidal), abundant secondary fascicles covering one-third to half of the internode length, wide carpogonia (13–15 µm in diameter) with pear- or bottle-shaped trichogyne and distribution restricted to Madagascar.

**Representative sequences in GenBank:** MT109273 (COI-5P); MT109263 (*rbcL*).

**Distribution:** Africa: Madagascar (Fig. 5.6).

**Key reference:** Fischer et al. (2020).

**Remarks:** the species was first described as the sole representative of a new genus (*Ahidranoa*) by Fischer et al. (2020) but the phylogenetic relationship (Fig. 5.9) and morphology (Fig. 5.10e–h) provide evidence of its similarity with the two previously described species of *Nocturama*. Thus, it is here proposed to be transferred to *Nocturama*.

*Nocturama novamundensis* Necchi and Entwisle, *Phytotaxa* 278:274 (2016) (Fig. 5.10i–l)

**Type:** SJRP29741, CCZ Branco et al., 18.viii.2007 (Holotype); MEL 2401959 (Isotype).

**Type locality:** Brazil: Rio Grande do Sul, Parque Estadual Florestal do Turvo, Tigre River, 27.206944° S, 53.833889° W.

**Description:** thalli dioecious; whorls contiguous or separated, spherical, or barrel-shaped, 300–535 µm in diameter; primary fascicles curved, with 8–15 cylindrical, ellipsoidal, or cylindrical cells; secondary fascicles absent or few and near the node; spermatangia 3.5–6 µm; carpogonial branches straight, composed of 3–10 cylindrical or ellipsoidal cells, developing from periaxial or proximal cells of primary fascicles, 30–70 µm in length; carpogonia with sessile and clavate trichogynes, 13–25.5 µm in length, 4–7 µm in diameter; carposporophytes 1–2



per whorl, 75–175  $\mu\text{m}$  in diameter; gonimoblast filaments with 3–5 barrel-shaped or short-cylindrical cells; carposporangia obovoidal, 10–18  $\mu\text{m}$  in length, 7–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinct from the others of the genus by the presence of non-audouinelloid primary fascicles with cells variable in shape (cylindrical, ellipsoidal, or obovoidal), secondary fascicles absent or few and present only near the nodes, narrow carpogonia (4–7  $\mu\text{m}$  in diameter) with clavate trichogyne and distribution restricted to Brazil.

**Representative sequences in GenBank:** KX764639, KX764640 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.6).

**Key reference:** Necchi et al. (2016).

*Volatus* IS Chapuis and ML Vis, Phycologia 56:457 (2017)

**Type species:** *Volatus personatus* IS Chapuis and ML Vis, Phycologia 56: 458 (2017).

**Description:** thalli monoecious, mucilaginous consistency; branching irregular; whorls well developed or reduced; cortical filaments of the main axis brown-colored with cylindrical cells; primary fascicles with ellipsoidal or fusiform cells; secondary fascicles few and sparse to abundant and covering the entire internode; spermatangia terminal or sub-terminal on primary or secondary fascicles; carpogonial branches well differentiated from fascicle cells, curved, twisted, or spirally coiled, arising from the periaxial or proximal cells, short, composed of disc- or barrel-shaped cells; involucrel filaments short and scarce, composed of ellipsoidal or spherical cells; carpogonia with sessile, lanceolate, cylindrical or clavate trichogynes; carposporophytes axial, large, one per whorl, hemispherical to spherical; gonimoblast filaments densely arranged, composed of cylindrical cells; carposporangia large, ellipsoidal, or obovoidal.

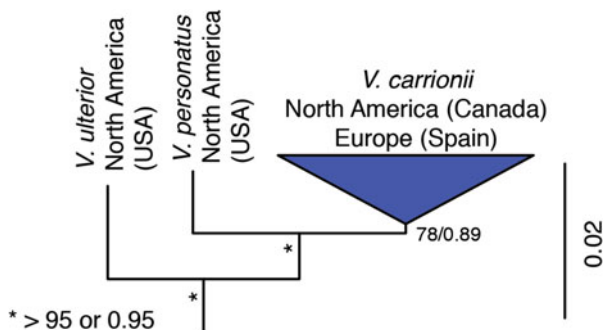
**Diagnostic characters:** this genus can be distinguished from all others in the Batrachospermales based on the characteristic of curved, twisted, or spirally coiled carpogonial branches, but cannot be distinguished from *Kumanoa* without DNA sequence data.

**Habitat:** species of this genus have been collected from streams within maritime and Mediterranean climates as well as those within the Appalachian mountain region. Environmental data are only available for *V. carrionii*, which was collected from streams with low conductivity (11.5–20  $\mu\text{S cm}^{-1}$ ), slightly acidic to neutral pH (6.5–7.1) and cool water temperature 14.2–19 °C.

**Distribution:** this genus is known from Europe and North America (Fig. 5.6).

**Phylogenetic relationships among species:** among the three species there is a single *rbcL* sequence for *V. personatus* and *V. ulterior* and four sequences for *V. carrionii* (Fig. 5.11). The phylogenetic analyses in Chapuis et al. (2017) show *V. personatus* and *V. carrionii* to be more closely related.

**Fig. 5.11** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Volatus*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities



Key to the species of the genus *Volatus*

1a	Whorls well developed with primary fascicles often composed of >7 cells	2
1b	Whorls reduced with primary fascicles composed of ≤7 cells	<i>V. ulterior</i>
2a	Carpogonia short, 25–50 μm in length, carposporangia obovoidal, distribution restricted to Europe or eastern Canada	<i>V. carrionii</i>
2b	Carpogonia long, 52–57 μm in length, carposporangia ellipsoidal, distribution restricted to southeastern USA	<i>V. personatus</i>

*Volatus carrionii* IS Chapuis and ML Vis, *Phycologia* 56:460 (2017) (Fig. 5.12a–c)

**Type:** GDA-A 8132, A Negro, 12.xi.2013 (Holotype), NY 02137794 (Isotype).

**Type locality:** Spain, Zamora, Río Negro, 42.064061° N, 6.413191° W.

**Description:** whorls well developed, confluent, barrel-shaped, 250–650 μm in diameter; primary fascicles 7–10 cells; carpogonial branches, twisted or spirally coiled, arising from the periaxial cells, >5 cells; carpogonia 25–50 μm in length with clavate to lanceolate trichogynes, 7–16 μm in diameter; carposporophyte 123–229 μm in diameter; gonimoblast filaments 2–3 cells; carposporangia obovoidal, 22–31 μm in length and 7–14 μm diameter.

**Diagnostic characters:** this species cannot be distinguished based on morphological characters from some species of *Kumanoa* with similar well-developed whorls such as *K. virgatodecaisneana* that has a similar distribution in eastern USA and Europe; DNA sequence data are needed for a positive identification.

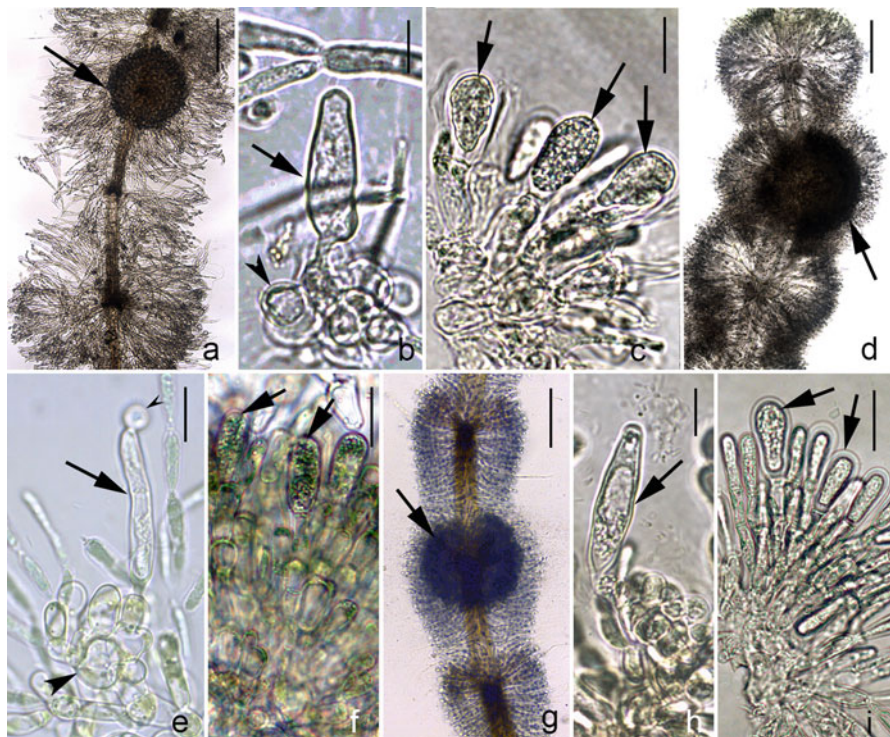
**Representative sequences in GenBank:** KM593866 (COI-5P); KM593860, KM593854 (*rbcL*).

**Distribution:** Europe: Spain; North America: Canada. (Fig. 5.6).

**Key reference:** Chapuis et al. (2017).

*Volatus personatus* IS Chapuis and ML Vis, *Phycologia* 56:458 (2017) (Fig. 5.12d–f)

**Type:** NY 02137795, RW Holton, 14.viii.2009 (Holotype), BHO A-0177, MICH 1210807 (Isotypes).



**Fig. 5.12** (a–c) *Volatus carrionii*: (a) whorl with carposporophyte (arrow); (b) carpogonium with clavate trichogyne (arrow) and a coiled carpogonial branch (arrowhead); (c) gonimoblast filaments with carposporangia (arrows); (d–f) *Volatus personatus*: (d) whorl with carposporophyte (arrow); (e) carpogonium with long cylindrical trichogyne (arrow) and attached spermatium (small arrowhead) and a coiled carpogonial branch (arrowhead); (f) gonimoblast filaments with carposporangia (arrows); (g–i) *Volatus ulterior*: (g) whorl with carposporophyte (arrow); (h) carpogonium with clavate trichogyne (arrow) and a coiled carpogonial branch (arrowhead); (i) gonimoblast filaments with carposporangia (arrows). Scale bars: (a, g) = 125  $\mu$ m; (b, h) = 10  $\mu$ m; (c, f, i) = 20  $\mu$ m; (d) = 150  $\mu$ m; (e) = 15  $\mu$ m (Image Author: Fig. (a–i) I Chapuis)

**Type locality:** the USA, Tennessee, Hiwassee River, 35.183333° N, 84.433333° W.

**Description:** whorls well developed, confluent, obovoid to barrel-shaped 410–510  $\mu$ m in diameter; primary fascicles 6–10 cells, secondary fascicles sparse; carpogonial branches primarily curved, but occasionally spirally coiled or straight arising from the periaxial or proximal cells, 4–7 cell; carpogonia 52–57  $\mu$ m in length with cylindrical trichogynes, 8–11  $\mu$ m in diameter; carposporophytes 195–405  $\mu$ m in diameter; gonimoblast filaments 3–4 cells; carposporangia ellipsoidal, 24–30  $\mu$ m in length and 11–14  $\mu$ m diameter.

**Diagnostic characters:** this species cannot be distinguished based on morphological characters from some species of *Kumanoa* with well-developed whorls such as

*K. americana* that is also reported from southeastern USA; DNA sequence data are needed for a positive identification.

**Representative sequences in GenBank:** KM593856 (*rbcL*).

**Distribution:** North America: the USA, known from the type locality only (Fig. 5.6).

**Key reference:** Chapuis et al. (2017).

**Remarks:** in the protologue (Chapuis et al. 2017), the carpogonial length was incorrect in the text (18–30  $\mu\text{m}$ ) and the scale bar for the photomicrographs (figs 8, 9) should have been 10  $\mu\text{m}$  not 20  $\mu\text{m}$  making the length similar to new measurements (52–57  $\mu\text{m}$ ) of the type specimen provided here.

*Volatus ulterior* IS Chapuis and ML Vis, Phycologia 56:460 (2017) (Fig. 5.12g–i)

**Type:** NY 02137796, K Goodman, 3.x.2009 (Holotype); BHO A-0233, MICH 1210808 (Isotypes).

**Type locality:** the USA, Georgia, Etowah River, 34.593056° N, 84.077778° W.

**Description:** whorls reduced, confluent, obconic, barrel-shaped, 200–345  $\mu\text{m}$  in diameter; primary fascicles 5–7 cells, secondary fascicles abundant; carpogonial branches primarily twisted or spirally coiled, occasionally curved arising from the periaxial or proximal cells, 5–6 cells; carpogonia 29–46  $\mu\text{m}$  in length with lanceolate, cylindrical, or clavate trichogynes, 8–11  $\mu\text{m}$  in diameter; carposporophytes 176–275  $\mu\text{m}$  in diameter; gonimoblast filaments 1–2 cells; carposporangia ellipsoidal, 18–29  $\mu\text{m}$  in length and 8–13  $\mu\text{m}$  diameter.

**Diagnostic characters:** this species may be distinguished morphologically from the other *Volatus* species by having reduced whorls and shorter primary fascicle cell number ( $\leq 7$  cells); however, it could be misidentified with some species of *Kumanoa* with similar obconic whorls such as *K. faroensis* also known from eastern USA. DNA sequence data are needed for a positive identification.

**Representative sequences in GenBank:** KM593870 (COI-5P); KM593852 (*rbcL*).

**Distribution:** North America (USA), known from the type locality only (Fig. 5.6).

**Key reference:** Chapuis et al. (2017).

## Genus *Batrachospermum*

*Batrachospermum* Roth, Bemerkungen über das Studium der cryptogamischen Wassergewächse:36 (1797a)

**Type species:** *Batrachospermum gelatinosum* (L) DC, Bull Sci (Soc Philomat Paris) 3:21 (1801).

**Description:** thalli monoecious or dioecious; olive-drab, sometimes brownish; consistency mucilaginous, branching irregular; whorls well developed; cortical filaments of the main axis with cylindrical cells; primary fascicles with ellipsoidal or fusiform cells; secondary fascicles few and sparse; spermatangia typically at the tips of primary, less often of secondary fascicles, but can be at the tips of

involucral filaments of the carpogonial branches, spherical to sub-spherical; carpogonial branches 40.5–65.9  $\mu\text{m}$  in length, composed of cells similar to the fascicles, straight, developing from the periaxial, proximal cells of primary fascicles, and occasionally from distal cells of primary fascicles; involucral filaments, short or long, composed of cylindrical or ellipsoidal cells; carpogonia with sessile, rarely stalked, clavate, lanceolate, or ellipsoidal trichogynes; carposporophytes pedunculate, spherical, inserted within the whorls or exerted, small; gonimoblast filaments densely arranged, composed of 2–4 barrel-shaped to cylindrical cells; carposporangia spherical to obovoidal.

**Diagnostic characters:** this genus can be differentiated from most other genera by its carpogonial branch being composed of cells similar in shape and size to primary fascicle cells and pedunculate carposporophytes; however, those characteristics are shared with the genus *Sheathia*. *Batrachospermum* can be distinguished from the seven *Sheathia* species with heterocortication (cortical filaments composed of cylindrical and bulbous cells), but not from *Sheathia* species with homocortication (cortical filaments are composed of cylindrical cells only); it can only be distinguished from those *Sheathia* species based on DNA sequence data and/or geographic distribution.

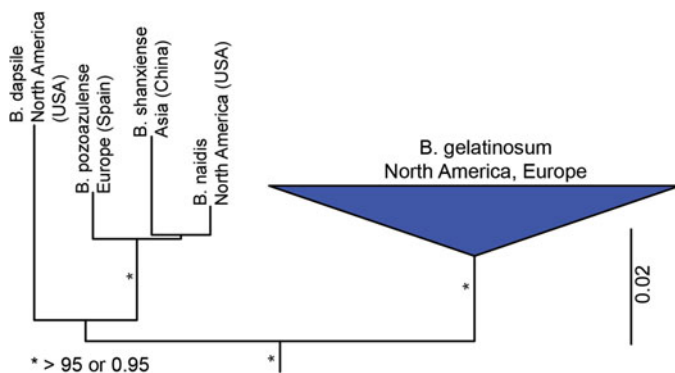
**Habitat:** this genus has a wide ecological distribution and can be collected in streams of tundra, boreal forest and temperate regions of North America, boreal forest, temperate and Mediterranean climate regions of Europe as well as temperate Asia. Habitat characteristics for *B. dapsile* from the type locality include pH 8.5, water temperature 17 °C, and conductivity 50  $\mu\text{S cm}^{-1}$ . Likewise, habitat characteristics for *B. pozoazulense* include pH 7.2–8.4, water temperature 11–15 °C, and conductivity 436–598  $\mu\text{S cm}^{-1}$ . For *B. pulchrum*, stream characteristics for two streams were as follows: streams small, shallow, and slow flowing with colorless water and alkaline pH 7.9–8.2, warm temperature of 21–23 °C, and variable conductivity 50–180  $\mu\text{S cm}^{-1}$ . Lastly, *B. gelatinosum* with its wide geographic distribution has been reported to have wide ecological tolerance with acidic to alkaline pH (5.0–8.4), water temperature 0–19 °C, and conductivity 0–490  $\mu\text{S cm}^{-1}$ , current velocities 0–106  $\text{cm s}^{-1}$ , and water from colorless to brown.

**Distribution:** *Batrachospermum* has been reported to date from northern hemisphere on three continents: Asia, Europe, North America. (Fig. 5.13). One species is relatively widespread (*B. gelatinosum*), whereas all others have a restricted distribution.

**Phylogenetic relationships among species:** there are *rbcL* sequences for five species currently recognized in *Batrachospermum* sensu stricto, *B. dapsile*, *B. gelatinosum*, *B. naiadis*, *B. pozoazulense*, and *B. shanxiense* (Fig. 5.14). *B. naiadis*, *B. pozoazulense*, and *B. shanxiense* are closely related with *B. dapsile* and *B. gelatinosum* more distant. There is one species (*B. pulchrum*) without sequence data that is distinguished by morphology.



**Fig. 5.13** Map showing the distribution of *Batrachospermum* species. Open symbols represent the type localities



**Fig. 5.14** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Batrachospermum*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

Key to the species of the genus *Batrachospermum*

1a	Monosporangia in rosettes originating from periaxial or proximal cells	<i>B. dapsile</i>
1b	Without monosporangia or if present, at the tips of fascicles	2
2a	Fascicles well curved, distribution in Caribbean islands	<i>B. pulchrum</i>
2b	Fascicles straight, distribution in Europe, North America, and Asia	3

(continued)



3a	Carpogonia with ellipsoidal trichogynes, known distribution in Asia (China)	<i>B. shanxiense</i>
3b	Carpogonia with clavate or lanceolate trichogynes, known distribution in Europe and North America	4
4a	Primary fascicles with 12–19 cells, known distribution in Europe (Spain)	<i>B. pozoazulense</i>
4b	Primary fascicles with 6–14 cells, known distribution in Europe and North America	<i>B. gelatinosum</i> and <i>B. naiadis</i> <sup>a</sup>

<sup>a</sup>*B. naiadis* cannot be distinguished from *B. gelatinosum* based on morphology or geography

***Batrachospermum dapsile*** IS Chapuis and ML Vis, *Phycologia* 56:460 (2017) (Fig. 5.15a–d)

**Type:** NY 02137798, E Salomaki, D Lam, and M Ashworth, 17.vii.2011 (Holotype), BHO A-0890, MICH1210805 (Isotypes).

**Type locality:** the USA, Oregon, Blue River, 44.56167° N, 122.40583° W.

**Description:** thalli dioecious; whorls spherical, separate, 268–498 µm in diameter; primary fascicles 6–12 cell; spermatangia 6–7 µm in diameter; carpogonial branches arising from the periaxial cells, 2–4 cells; carpogonia 34–58 µm in length with lanceolate, inflated-lanceolate trichogynes, 17–25 µm in diameter; carposporophytes 1–2 per whorl, (76–)104–155 µm in diameter; carposporangia obovoidal, 12–15.3 µm in length and 7.2–9 µm diameter. Male thalli with monosporangia terminal on short primary fascicles arising from periaxial or proximal cells forming a mass of cells arranged in rosettes near the center of the whorl, 9–14 µm in length and 6–9(–11) µm diameter.

**Diagnostic characters:** this species can be distinguished from other *Batrachospermum* species based on the rosettes of monosporangia from periaxial/proximal cells on the male thalli only.

**Representative sequences in GenBank:** KM593871 (COI-5P); KM593855 (*rbcl*).

**Distribution:** North America (USA), known from the type locality only (Fig. 5.13).

**Key reference:** Chapuis et al. (2017).

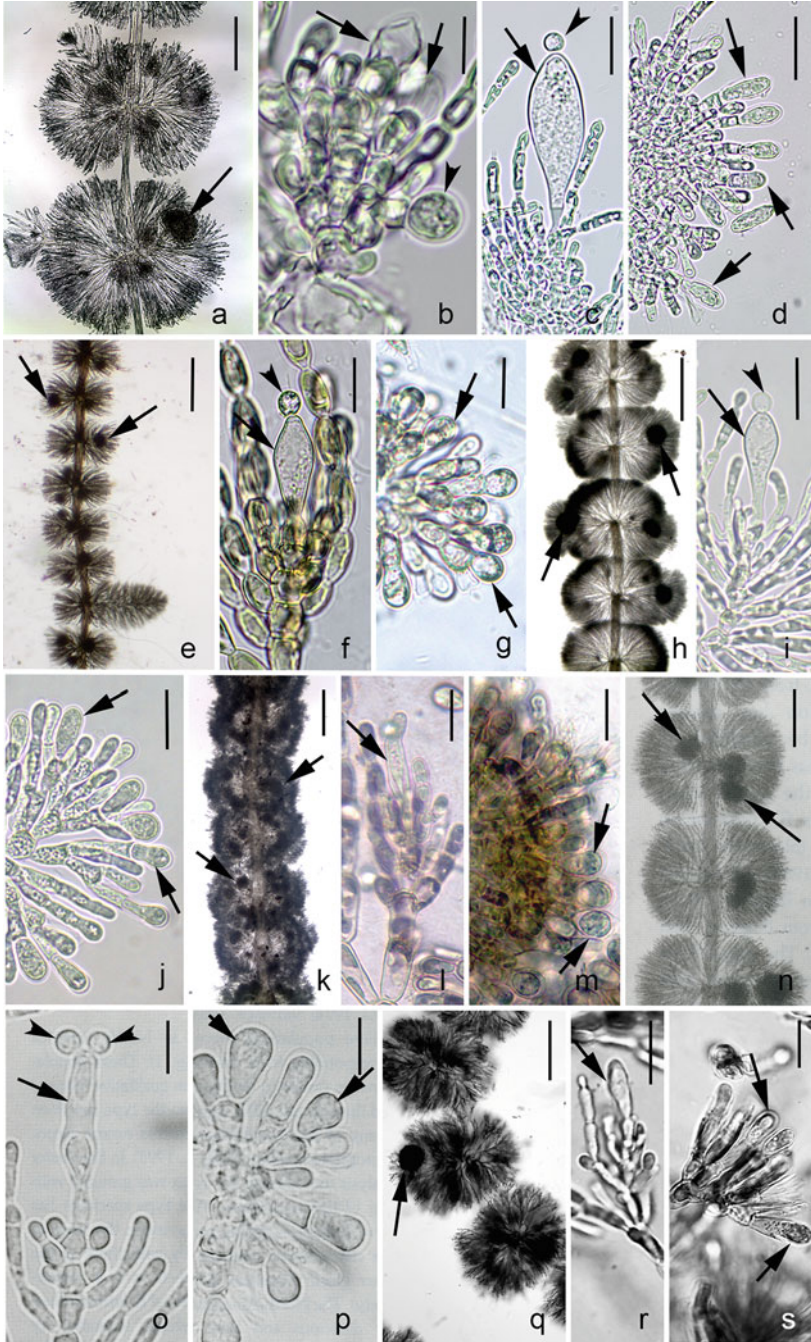
**Remarks:** the description has been revised from the protologue to clarify that the monosporangia are on the male thalli and reflect new measurements for whorls, carpogonia, spermatangia, and carposporangia from the type material; there have been previously described species in the genus with monosporangia, but none with this unusual arrangement in rosettes.

***Batrachospermum gelatinosum*** (L) DC, *Bull Sci (Société Philomathique de Paris)* 3:21 (1801) (Fig. 5.15e–g)

**Basionym:** *Conferva gelatinosa* L, *Species plantarum* Vol. 2:1166 (1753).

**Type:** OXF, specimen on which tab. 7 fig. 42 from Dillenius's *Historia Muscorum* is based (Lectotype) designated by Compère (1991:22).

**Type locality:** presumably Great Britain in northern Europe.



**Fig. 5.15** (a–d) *Batrachospermum dapsile*: (a) spherical whorls with spherical, pedunculate carposporophyte (arrow); (b) cluster of short cells with monosporangia remnants (arrows) and monosporangium (arrowhead) at tips; (c) fertilized carpogonium with lanceolate trichogyne (arrow) and attached spermatium (arrowhead); (d) carposporophyte with ellipsoidal

**Description:** thalli monoecious; whorls spherical, barrel-shaped, separate, or contiguous, (138–)350–800(–1100)  $\mu\text{m}$  in diameter; primary fascicles 7–14 cells; spermatangia typically terminal on fascicles, in some populations at the tips of involucrel filaments of the carpogonial branches, 5–7  $\mu\text{m}$  in diameter; carpogonial branches 3–10 cells; carpogonia (18–)24–55(–68)  $\mu\text{m}$  in length with clavate or lanceolate trichogynes (5–)6.5–14(–17) in diameter; carposporophytes 1–7(–11) per whorl, (40–)60–143  $\mu\text{m}$  in diameter; carposporangia obovoidal, 8–16  $\mu\text{m}$  in length and 6–12  $\mu\text{m}$  diameter.

**Diagnostic characters:** specimens attributable to this species based on DNA data have been reported with a wide range in morphological characteristics. This species cannot be distinguished from *B. naiadis* in this genus and homocorticate *Sheathia* species.

**Representative sequences in GenBank:** GU810830, KM270675, KM592957 (COI-5P); DQ787560, GU810833, KJ825970 (*rbcl*).

**Distribution:** widespread in North America: the USA and Canada; widespread in Europe: Belgium, Estonia, Finland, France, Great Britain, Italy, Latvia, Lithuania, Norway, Poland, Spain (Fig. 5.13).

**Key references:** Vis et al. (1995, 1996a), Vis and Sheath (1997), Eloranta et al. (2011), Abdelahad et al. (2015).

**Remarks:** this species has been reported from locations worldwide but only confirmed using DNA sequence data from Europe and North America. The description combines morphological measurements provided for specimens with DNA sequence data (House et al. 2010; Abdelahad et al. 2015) as well as Vis et al. (1995) and Eloranta et al. (2011). Previous reports from Australasia were determined to be a new species based on DNA sequence data, currently named *Nothocladus pseudogelatinosus* (Entwistle et al. 2004, 2016). Spermatangia on

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**Fig. 5.15** (continued) carposporangia (arrows); (e–g) *Batrachospermum gelatinosum*: (e) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (f) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (g) carposporophyte with obovoidal or spherical carposporangia (arrows); (h–j) *Batrachospermum naiadis*: (h) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (i) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (j) carposporophyte with obovoidal, ellipsoidal carposporangia (arrow); (k–m) *Batrachospermum pozoazulense*: (k) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (l) carpogonium with ellipsoidal trichogyne (arrow); (m) carposporophyte with obovoidal carposporangia (arrows); (n–p) *Batrachospermum pulchrum*: (n) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (o) fertilized carpogonium with ellipsoidal trichogyne (arrow) and attached spermatia (arrowheads); (p) carposporophyte with obovoidal carposporangia (arrows); (q–s) *Batrachospermum shanxiense*: (q) barrel-shaped whorls with spherical, pedunculate carposporophyte (arrow); (r) carpogonium with ellipsoidal trichogyne (arrow); (s) carposporophyte with ellipsoidal carposporangia (arrows). Scale bars: (a) = 150  $\mu\text{m}$ ; (b, o–p) = 10  $\mu\text{m}$ ; (c, d, i, j, l, s) = 20  $\mu\text{m}$ ; (e) = 250  $\mu\text{m}$ ; (f, g, m, r) = 15  $\mu\text{m}$ ; (h) = 500  $\mu\text{m}$ ; (k) = 300  $\mu\text{m}$ ; (n, q) = 200  $\mu\text{m}$  (Image author: Fig. (k, l) I Chapuis; Fig. (n–p) reprinted with permission by the Taylor and Francis from Vis et al. (1996b); Fig. (q, r) reprinted with permission by Taylor and Francis from Chapuis et al. (2017))

the involucrel filaments of the carpogonial branches have been reported for some populations and *B. gelatinosum* f. *spermatoinvolucrum* was previously proposed; specimens with this morphology may have *rbcL* sequence data identical to other *B. gelatinosum* specimens without this character or vary somewhat (~1.9% divergence) (Vis and Sheath 1998; Abdelahad et al. 2015). Misshaped or deformed trichogynes have been noted in populations from locations with high nutrient content in the waters (Abdelahad et al. 2015).

***Batrachospermum naiadis*** IS Chapuis and ML Vis, *Phycologia* 56:461 (2017) (Fig. 5.15h–j)

**Type:** NY Voucher Barcode 02137797, ML Vis, and D House, 22.x.2009 (Holotype); BHO A-0076, MICH1210806 (Isotypes).

**Type locality:** the USA, Virginia, Spring in Front Royal, 38.937056° N, 78.184444° W.

**Description:** thalli monoecious, purple-colored; whorls slightly separate, spherical, barrel-shaped, 570–980 µm in diameter; primary fascicles 9–12 cells often with apical hairs; spermatangia 5–6 µm in diameter; carpogonial branches 5–7 cells; carpogonia 24–43 µm in length with clavate to inflated-clavate stalked trichogynes, 7–13 µm in diameter; carposporophytes 1–4 per whorl, 102–218 µm in diameter; carposporangia obovoidal, 11–18 µm in length and 6–9 µm diameter.

**Diagnostic characters:** this species cannot be distinguished based on morphology from *Batrachospermum gelatinosum* and their geographic ranges overlap such that DNA sequence data are needed for a positive identification.

**Representative sequences in GenBank:** KM593872 (COI-5P); KM593857 (*rbcL*).

**Distribution:** North America: the USA, known from the type locality only (Fig. 5.13).

**Key reference:** Chapuis et al. (2017).

**Remarks:** habitat characteristics for this species from the type locality include pH 7.2, water temperature 13 °C, and conductivity 830 µS cm<sup>-1</sup>.

***Batrachospermum pozoazulense*** IS Chapuis and ML Vis, *Phycologia* 56:465 (2017) (Fig. 5.15k–m)

**Type:** GDA-A8362, B Esteban, 5.x.2013 (Holotype); NY 02137799 (Isotype).

**Type locality:** Spain, Burgos, Covanera, Tubilla del Agua, Pozo Azul, 42.735833° N, 3.795833° W.

**Description:** thalli monoecious; whorls barrel-shaped, spherical, contiguous, 533–695 µm in diameter; primary fascicles 12–19 cells; spermatangia 6–10 µm in diameter; carpogonial branches 3–7 cells; carpogonia (30–)33–57(–67) µm in length with clavate trichogynes, 7–15 µm in diameter; carposporophytes 1–7 per whorl, 50–173 µm in diameter; carposporangia spherical or obovoidal, 9–17 µm in length and 6–11 µm diameter.

**Diagnostic characters:** this species cannot be distinguished based on morphology from *Batrachospermum gelatinosum* and their geographic ranges overlap such that DNA sequence data are needed for a positive identification.

**Representative sequences in GenBank:** KM593867 (COI-5P); KM593858 (*rbcL*).

**Distribution:** Europe: Spain (5.3.1).

**Key reference:** Chapuis et al. (2017).

*Batrachospermum pulchrum* Sirodot, Les Batrachospermes:225 (1884)

(Fig. 5.15n–p)

**Type:** PC0591654, Mazé and Schramm, 15.viii.1868 (Lectotype here designated); PC0591656 (Isolectotypes).

**Type locality:** Guadeloupe, à Matouba, rivière des Ecrevisses et l'un de ses petits affluents, 16.042925° N, 61.695320° W (estimated).

**Description:** thalli monoecious; whorls spherical, separate, 296–485 µm in diameter; primary fascicles well curled, with (5–)10–13 cells; spermatangia terminal on fascicles and involucrel filaments of carpogonial branches, 5–6 µm in diameter; carpogonial branches 4–6 cells; carpogonia 17–32 µm in length, with lanceolate, cylindrical trichogynes, 4–7 µm diameter; carposporophytes 1–3 per whorl, 59–144 µm in diameter; carposporangia obovoidal, (9–)11–15 µm in length and (6–)9–11 µm diameter.

**Diagnostic characters:** the primary character distinguishing this species is the well-curled fascicles; a secondary character is the spermatangia on the tips of the involucrel filaments of the carpogonial branch, but this character is shared with *B. gelatinosum* (referred to as *B. gelatinosum* f. *spermatoinvolucrum*).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** North America: Lesser Antilles: Guadeloupe, Martinique, and Grenada (Fig. 5.13).

**Key references:** Sirodot (1884), Vis et al. (1995, 1996b).

**Remarks:** the description is based on the measurements from Vis et al. (1995, 1996b) with spermatangia taken from the photographic plate; some of the measurements in the description in Vis et al. (1995) are incorrect but correct in the morphological table in that paper.

*Batrachospermum shanxiense* SL Xie, IS Chapuis, and ML Vis, Phycologia 56:465 (2017) (Fig. 5.15q–s)

**Type:** SXU SAS-06146 SL Xie, J Feng, and G Yao, vi.2006 (Holotype).

**Type locality:** China, Shanxi, spring in the source of Fen River, 38.922877° N, 112.177794° E.

**Description:** thalli monoecious; whorls spherical, separate, 485–560 µm in diameter; primary fascicles 8–11 cells; spermatangia 5–10 µm in diameter; carpogonial branches 6–7 cells; carpogonia 20–45 µm in length with ellipsoidal trichogynes, 5–10 µm in diameter; carposporophytes one to several per whorl, 100–150 µm in diameter; carposporangia obovoidal, 14–19 µm in length and 7–11 µm diameter.

**Diagnostic characters:** this species cannot be distinguished based on morphology from *Batrachospermum gelatinosum* but may be distinguished using geographic ranges; DNA sequence data are recommended for a positive identification.

**Representative sequences in GenBank:** KM593869 (COI-5P); KM593851 (*rbcL*).



**Distribution:** Asia: China, known from the type locality only (Fig. 5.13).

**Key reference:** Chapuis et al. (2017).

### *Doubtful Species*

*Batrachospermum carpocontortum* Sheath, MO Morison, KM Cole and Vanalst, Phycologia 25:325 (1986). This species was originally distinguished based on carpogonia with trichogynes that had protrusions and bends. Recent research has shown with DNA data that populations with aberrant trichogyne morphology are genetically similar to those without it and hypothesized these deformities may be due to environmental conditions especially increased nutrients (Abdelahad et al. 2015).

*Batrachospermum desikacharyi* V Sankaran, Phycos 23:169 (1984). The distinguishing character for this species described from India is a corticated carposporophyte branch. The drawing in the protologue shows expanded cells of the branch with some filaments winding around the branch. This type of carpogonial branch is similar to that in *Montagnia*. In addition, measurements of morphological characters, especially the size of the carposporangia, are consistent with *M. macrospora*, which is known to occur in Asia. However, there are inexplicable inconsistencies in measurements of the type specimen between the protologue and Sheath et al. (1994c).

*Batrachospermum heteromorphum* ZX Shi, ZY Hu, and Kumano, Jap J Phycol 41:295 (1993). This species was distinguished from related species based on whorls of two types, barrel-shaped, spherical, and obconic, as well as the development of the trichogyne. The photomicrographs in the protologue show two thalli each with different whorl morphology, a thallus with abundant secondary fascicles along the length of the internode giving the whorls an obconic appearance and another with few secondary fascicles and a spherical appearance. It is unclear if these two thalli represent a potential mixed collection of two species. The trichogyne development in this species starts spatulate becomes clavate to lanceolate, which is supposedly in contrast to *B. gelatinosum* with trichogynes that are obovate when immature and become clavate to lanceolate. Neither of these characteristics is sufficient to warrant species status.

*Batrachospermum lochmodes* Skuja, Arch Hydrobiol Suppl 15:620 (1938). This species is distinguished from most other species of the genus by having monosporangia at the tips of primary and secondary fascicles. These monosporangia were reported to be obovoidal and larger than typical spermatangia. However, no spermatangia were reported for the species. The monosporangia were only documented with drawings and researchers have been unable to locate specimens in relevant herbaria of RIG, UPS, C, Z, W. Therefore, it is difficult to ascertain whether to recognize this species. Of note is the type locality in Indonesia which is quite geographically distant from the locations of other species, *B. skujae* in Europe and *B. dapsile* in North America, noted to have monosporangia and therefore is unlikely to be synonymous.



***Batrachospermum nova-guineense*** Kumano and IM Johnstone, Jap J Phycol 31: 66 (1983). The morphological character used to distinguish this species from others in the genus is a slightly curved carpogonial branch. From the figures, it appears that this curvature is due to involucre filaments only developing on one side of the branch for some carpogonia only, but others are straight with involucre filaments on both sides. This morphological character only present in some carpogonial branches is not sufficient to warrant species status.

***Batrachospermum pengzhouense*** SL Xie and ZX Shi, Bull. Bot. Res. 24:131 (2004). This species was noted to be similar to *B. nova-guineense* and *Sheathia arcuata* (= *B. arcuatum*) in the protologue. In the description and from the drawings, there appear to be no unique morphological characters to distinguish this species from others in *Batrachospermum* or from *Sheathia* species with homocortication. In a later publication (Shi et al. 2006), it was distinguished from *S. arcuata* based on sub-cylindrical primary fascicle cells and carpogonial branches of 3–5 cells, but both those characters overlap and are not sufficient to distinguish this species from numerous others in both genera.

***Batrachospermum skujae*** Geitler, Öesterr Bot Z 93:127 (1944). This species is only distinguished from *Batrachospermum gelatinosum* based on the presence of putative monosporangia. However, the monosporangia dimensions are similar and only somewhat greater than spermatangia (7–10 µm in length and diameter, 5–7 µm in diameter, respectively), with spermatangia reported as rare and no measurements.

***Batrachospermum szechwanense*** CC Jao, Sinensia 12:264 (1941). This species was recognized as a distinct species based on a somewhat curved trichogyne. This species has been recently reported from India in addition to the type locality in China based on morphology (Perumal and Sundararaj 2019). The character of a somewhat curved trichogyne, a small variation in a single morphological character, alone is not sufficient for recognition as a distinct species.

***Batrachospermum trichocontortum*** Sheath and ML Vis, Phycology 35:131 (1996). This species was originally distinguished based on carpogonia with trichogynes that had tips undulated, capitate, or helically twisted. Recent research has shown that populations of *Batrachospermum gelatinosum* with and without aberrant trichogyne morphology are genetically similar. It is hypothesized these deformities may be due to environmental conditions, especially increased nutrients (Abdelahad et al. 2015).

***Batrachospermum trichofurcatum*** Sheath and ML Vis, Phycology 35:128 (1996). This species was originally distinguished based on carpogonia with trichogynes that were forked. This aberrant morphology is likely analogous to *B. trichocontortum* and due to environmental conditions (Abdelahad et al. 2015).

## Genus *Kumanoa*

***Kumanoa*** Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:709 (2009)

**Synonyms:** *Batrachospermum* section *Hybrida* De Toni, Sylloge Algar 4:63 (1897b); *Batrachospermum* section *Contorta* Skuja, Hedwigia 71:81 (1931). *Batrachospermum* section *Contorta* Skuja emend. Vis and Entwisle, J Phycol 36:1181 (2000).

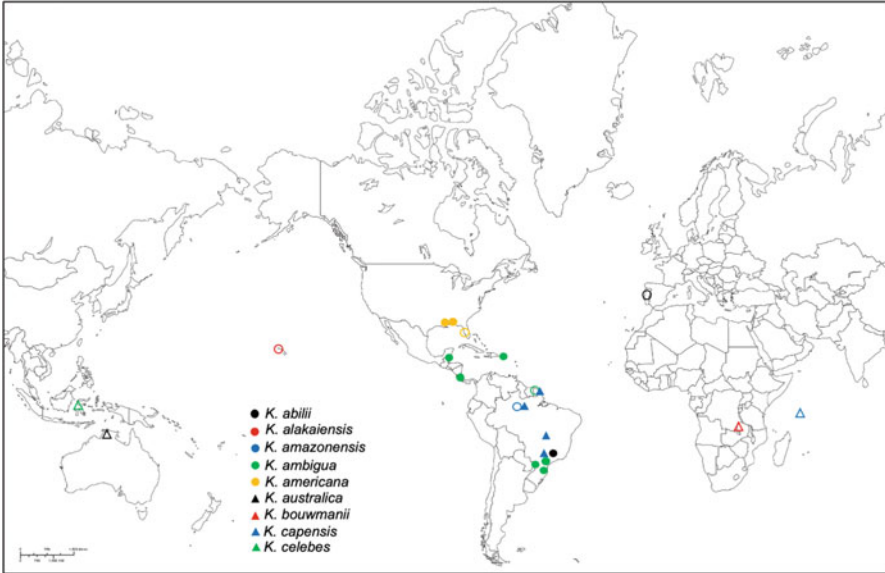
**Type species:** *Kumanoa virgatodecaisneana* (Sirodot) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:709 (2009).

**Description:** thalli monoecious, dioecious or polyecious, greenish, greenish-blue, or less often brownish; consistency mucilaginous; branching irregular or less often pseudodichotomous; whorls well developed, contiguous or separated, obconic, pear-shaped, spherical or barrel-shaped; cortical filaments of the main axis well developed with cylindrical cells; primary fascicles formed by cells variable in shape and length, ranging from cylindrical to ellipsoidal, obovoidal or pear-shaped or audouinelloid; secondary fascicles abundant and covering the entire internode or few and sparse near the nodes; spermatangia on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, helically coiled or curved, rarely straight, developing from the periaxial or proximal cells of primary fascicles, rarely from secondary fascicles or cortical filaments, short or long, composed of disc- or barrel-shaped cells; involucrel filaments, short, composed of 1–5 disc- or barrel-shaped cells, coiled around the carpogonial branches forming a knot; carpogonia with sessile or stalked, cylindrical, sub-cylindrical, clavate, or ellipsoidal trichogynes; carposporophytes axial, hemispherical, or spherical, lower or higher than the whorls, 1–2, rarely 3, per whorl, large; gonimoblast filaments of one type, densely or loosely arranged, composed of cylindrical, ellipsoidal, or barrel-shaped cells; carposporangia small or large, obovoidal, pear-shaped, sub-spherical or spherical, clavate or ellipsoidal.

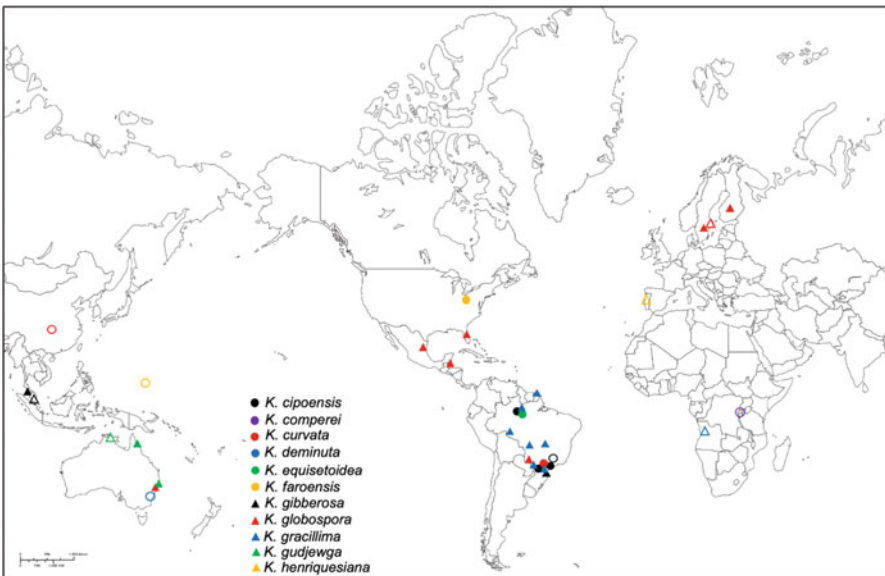
**Diagnostic characters:** the genus is characterized by having carpogonial branches well differentiated from the fascicles, spirally coiled or curved, rarely straight; carposporophytes axial, centrally inserted within the whorls; and gonimoblast filaments of one type, arising radially from the fertilized carpogonia. The three species of the genus *Volatus* shared the presence of curved, twisted, or spirally coiled carpogonial branches and can be misinterpreted as *Kumanoa*, particularly the species with curved or slightly twisted carpogonial branches (*K. abilii*, *K. celebes*, and *K. virgatodecaisneana*). They can be distinguished from *Kumanoa* only with DNA sequence data.

**Habitat:** species of *Kumanoa* occur in a wide range of environmental conditions, mostly in unpolluted waters, with slightly acidic to mildly alkaline pH, low to high ion content, moderately to well aerated and slow to fast flowing waters, on rocky substrates, tree logs, artificial substrates, or epiphytic on macrophytes, in open to shaded stream segments.

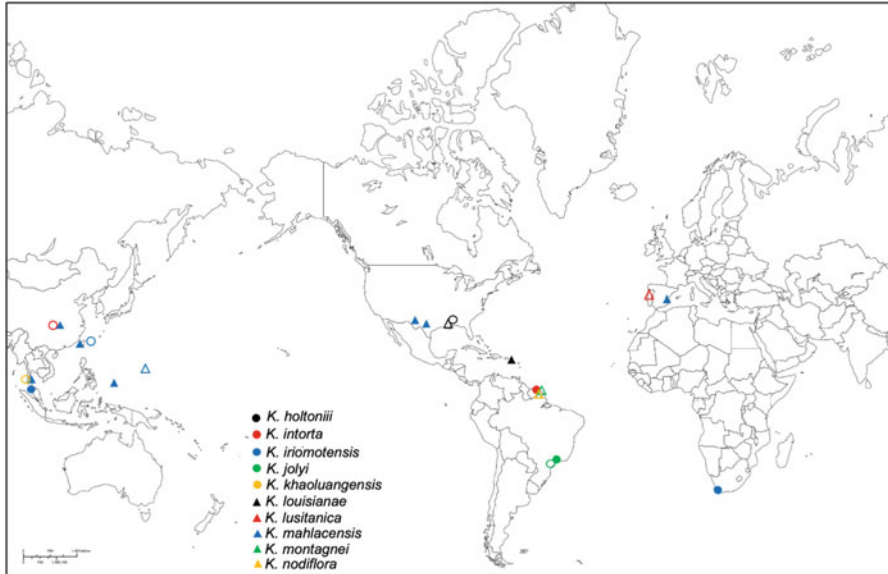
**Distribution:** representatives of the genus have been reported mainly in tropical or sub-tropical, less often in temperate regions of Africa, Asia, Australasia, Europe, North and South America (Figs. 5.16-5.19).



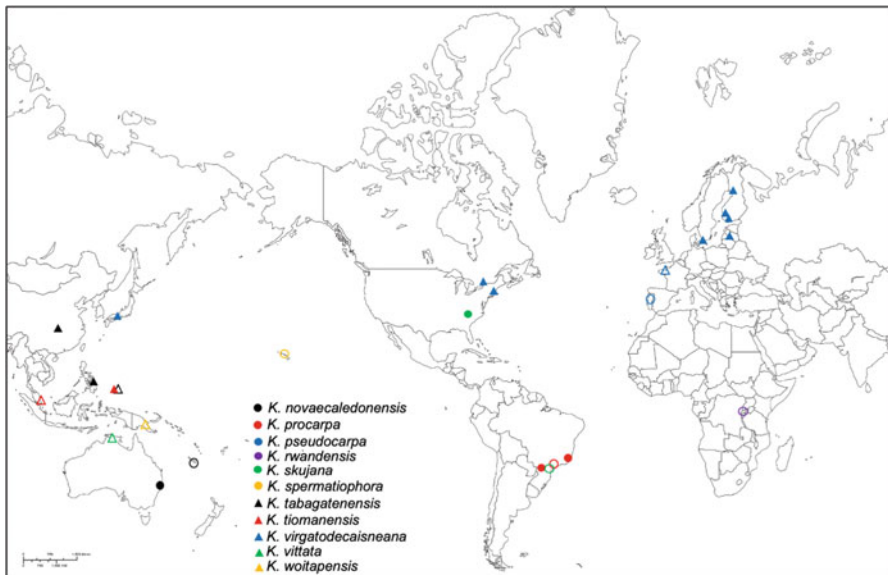
**Fig. 5.16** World map showing the distribution of the following species of *Kumanoa*: *K. abilii*, *K. alakaiensis*, *K. amazonensis*, *K. ambigua*, *K. americana*, *K. australica*, *K. bouwmanii*, *K. capensis*, and *K. celebes*. Open symbols represent the type localities



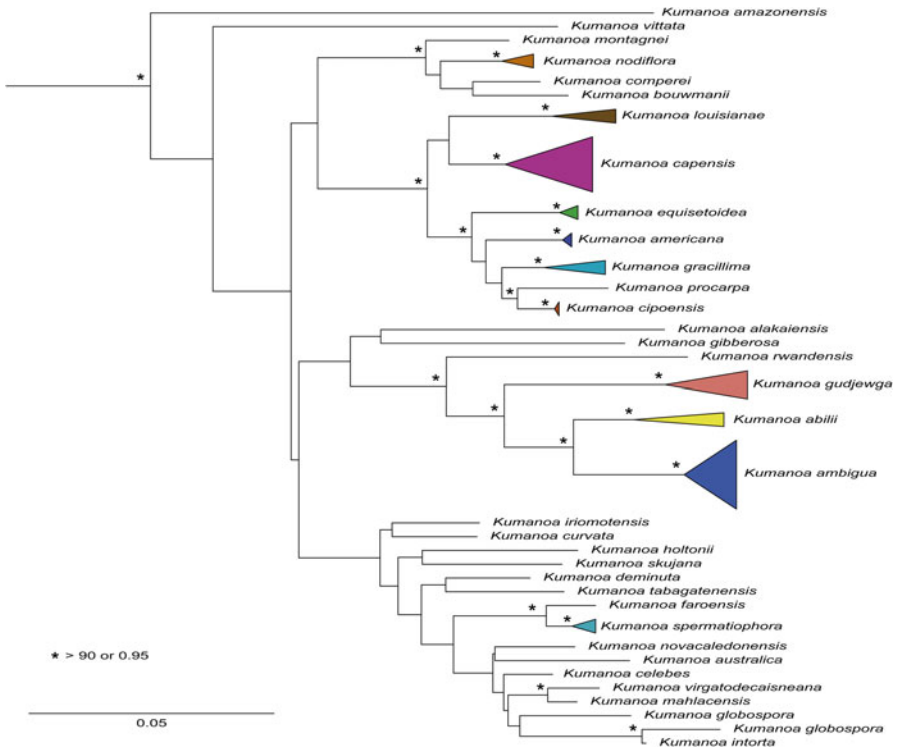
**Fig. 5.17** World map showing the distribution of the following species of *Kumanoa*: *K. cipoensis*, *K. curvata*, *K. deminuta*, *K. equisetoides*, *K. feroensis*, *K. gibberosa*, *K. globospora*, *K. gracillima*, *K. gudjewga*, and *K. henriquesiana*. Open symbols represent the type localities



**Fig. 5.18** World map showing the distribution of the following species of *Kumanoa*: *K. holtonii*, *K. intorta*, *K. iriomotensis*, *K. jolyi*, *K. khaoluangensis*, *K. louisianae*, *K. lusitanica*, *K. mahlacensis*, *K. montagnei*, and *K. nodiflora*. Open symbols represent the type localities



**Fig. 5.19** World map showing the distribution of the following species of *Kumanoa*: *K. novaecaledonensis*, *K. procarpa*, *K. pseudocarpa*, *K. skujana*, *K. spermatiophora*, *K. tabagatenensis*, *K. tiomanensis*, *K. virgatodecaisneana*, *K. vitatta*, and *K. woitapensis*. Open symbols represent the type localities



**Fig. 5.20** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Kumanoa*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences within the genus (Fig. 5.20) based on data reported by Vis et al. (2012), Necchi and Vis (2012), and recent publications of new species produced a tree with only a few well-supported clades including three or more species: a) two large clade including seven species (*K. americana*, *K. capensis*, *K. cipoensis*, *K. equisetoides*, *K. gracillima*, *K. louisianae*, and *K. procarpa*) and (*K. australica*, *K. celebes*, *K. globospora*, *K. intorta*, *K. mahlacensis*, *K. novaealedonensis*, and *K. virgatodecaisneana*); and b) two minor clades each including four species: 1) *K. bouwmanii*, *K. comperei*, *K. montagnei*, and *K. nodiflora*; 2) *K. abilii*, *K. ambigua*, *K. gudjewga*, and *K. rwandensis*. No clear geographic trends were evident with species from different continents being in well-supported clades (i.e., *K. montagnei* and *K. nodiflora* from South America with *K. bouwmanii* and *K. comperei* from Africa), and no sub-groups deserving a taxonomic status (e.g., sections) based on morphological similarities. There are seven species without sequence data that are distinguished by morphological characters only.

Key to the species of the genus *Kumanoa*

1a	Branching pseudodichotomous	2
1b	Branching irregular	11
2a	Whorls reduced, with 3–8(–9) cells	3
2b	Whorls well developed, with (6–)9–20 cells	6
3a	Whorls compact	<i>K. gibberosa</i>
3b	Whorls not compact	4
4a	Primary fascicles curved	<i>K. henriquesiana</i>
4b	Primary fascicles straight	5
5a	Carposporophytes lower or equal to whorls, carposporangia small ( $\leq 15 \mu\text{m}$ in length, $\leq 11 \mu\text{m}$ in diameter)	<i>K. louisianae</i>
5b	Carposporophytes higher than whorls, carposporangia large ( $\geq 15 \mu\text{m}$ in length, $\geq 10 \mu\text{m}$ in diameter)	<i>K. nodiflora</i>
6a	Primary fascicles audouinelloid	7
6b	Primary fascicles non-audouinelloid	<i>K. tabagatenensis</i>
7a	Carposporophytes loose	8
7b	Carposporophytes dense	9
8a	Secondary fascicles absent or few; carposporangia large ( $\geq 20 \mu\text{m}$ in length, $\geq 17 \mu\text{m}$ in diameter)	<i>K. equisetoides</i>
8b	Secondary fascicles abundant, covering the entire internode; carposporangia small ( $\leq 15 \mu\text{m}$ in length, $\leq 10.5 \mu\text{m}$ in diameter)	<i>K. procarpa</i>
9a	Carposporophytes higher than whorls, large ( $\geq 350 \mu\text{m}$ in diameter, $\geq 250 \mu\text{m}$ in height)	<i>K. cipoensis</i>
9b	Carposporophytes lower than whorls, small ( $\leq 240 \mu\text{m}$ in diameter, $\leq 130 \mu\text{m}$ in height)	10
10a	Carpogonia short ( $\leq 37 \mu\text{m}$ in length); carposporangia obovoidal ( $\geq 12 \mu\text{m}$ in length)	<i>K. americana</i>
10b	Carpogonia long ( $\geq 37 \mu\text{m}$ in length); carposporangia spherical or sub-spherical ( $\leq 12 \mu\text{m}$ in length)	<i>K. tiomanensis</i>
11a	Monosporangia present	12
11b	Monosporangia absent	15
12a	Monosporangia small ( $\leq 15 \mu\text{m}$ in length), occurring on primary and secondary fascicles	13
12b	Monosporangia large ( $\geq 20 \mu\text{m}$ in length), occurring on specialized structures	14
13a	Carpogonia short ( $\leq 40 \mu\text{m}$ in length); carposporophytes dense and higher than the whorls	<i>K. intorta</i>
13b	Carpogonia long ( $\geq 45 \mu\text{m}$ in length); carposporophytes loose and lower than the whorls	<i>K. waitapensis</i>
14a	Monosporangia forming rings around the nodes on the axes; thalli dioecious	<i>K. lusitanica</i>
14b	Monosporangia forming globose structures resembling carposporophytes; thalli monoecious	<i>K. pseudocarpa</i>
15a	Spermatangia on specialized branches	16
15b	Spermatangia on ordinary primary or secondary fascicles	17
16a	Spermatangia on shorter fascicles, carposporophytes dense	<i>K. vittata</i>

(continued)



16b	Spermatangia on colorless fascicles cells (spermatophores), carposporophytes loose	<i>K. spermatophora</i>
17a	Whorls reduced, secondary fascicles lacking	18
17b	Whorls reduced or well developed; secondary fascicles abundant, covering half to the entire internode	19
18a	Whorls compact, carposporophytes dense	<i>K. amazonensis</i>
18b	Whorls not compact, carposporophytes loose	<i>K. khaoluangensis</i>
19a	Primary fascicles curved	20
19b	Primary fascicles straight	23
20a	Primary fascicles reduced, with (4–)5–7(–8) cells	<i>K. alakaiensis</i>
20b	Primary fascicles well developed, with 6–20 cells	21
21a	Primary fascicles with 6–12 cells, carpogonial branches curved or slightly twisted	<i>K. curvata</i>
21b	Primary fascicles with 13–20 cells, carpogonial branches helically twisted	22
22a	Carpogonia short ( $\leq 40 \mu\text{m}$ in length), carposporophytes dense and lower than whorls	<i>K. jolyi</i>
22b	Carpogonia long ( $\geq 40 \mu\text{m}$ in length), carposporophytes loose and higher than whorls	<i>K. skujana</i>
23a	Distal fascicle cells thin (length/diameter $\geq 2.5$ ), elongate-ellipsoidal or fusiform	24
23b	Distal fascicle cells thick (length/diameter $\leq 2.5$ ), ellipsoidal, obovoidal, pear-shaped, or sub-spherical	30
24a	Known distribution in continental Africa	25
24b	Known distribution in other continents	26
25a	Whorls reduced, with 5–8 obovoidal or ellipsoidal cells	<i>K. bouwmanni</i>
25b	Whorls well developed, with 8–11 ellipsoidal or fusiform cells	<i>K. rwandensis</i>
26a	Carpogonial branches long ( $\geq 15$ cells)	<i>K. australica</i>
26b	Carpogonial branches short ( $\leq 12$ cells)	27
27a	Carpogonia long ( $\geq 40 \mu\text{m}$ in length)	27
27b	Carpogonia short ( $\leq 40 \mu\text{m}$ in length)	29
28a	Carposporophytes large ( $\geq 350 \mu\text{m}$ in diameter and $\geq 190 \mu\text{m}$ in height)	<i>K. capensis</i>
28b	Carposporophytes small ( $\leq 230 \mu\text{m}$ in diameter and $\leq 100 \mu\text{m}$ in height)	<i>K. montagnei</i>
29a	Carposporophytes loose; carposporangia small ( $\leq 13 \mu\text{m}$ in length, $\leq 11 \mu\text{m}$ in diameter)	<i>K. globospora</i>
29b	Carposporophytes dense; carposporangia large ( $> 13 \mu\text{m}$ in length, $\geq 11.5 \mu\text{m}$ in diameter)	<i>K. iriomotensis</i>
30a	Whorls reduced, with 4–7(–11) cells	31
30b	Whorls well developed, with (6–)8–15 cells	35
31a	Carpogonial branches short ( $\leq 8$ cells)	31
31b	Carpogonial branches long ( $\geq 8$ cells)	34
32a	Carpogonia short ( $\leq 35 \mu\text{m}$ in length)	<i>K. comperei</i>
32b	Carpogonia long ( $\geq 42 \mu\text{m}$ in length)	32
33a	Carposporophytes small ( $\leq 270 \mu\text{m}$ in diameter, $\leq 170 \mu\text{m}$ in height), carposporangia large ( $\geq 17 \mu\text{m}$ in length, $\geq 17 \mu\text{m}$ in diameter)	<i>K. holtonii</i>

(continued)

33b	Carposporophytes large ( $\geq 250 \mu\text{m}$ in diameter, $\geq 130 \mu\text{m}$ in height), carposporangia small ( $\leq 17 \mu\text{m}$ in length, $\leq 12 \mu\text{m}$ in diameter)	<i>K. gracillima</i>
34a	Known distribution in Australasia	<i>K. deminuta</i>
34b	Known distribution in Asia, Europe, and North America	<i>K. mahlacensis</i>
35a	Carpogonial branches straight, curved, or slightly twisted	36
35b	Carpogonial branches helically twisted	38
36a	Carpogonia short ( $\leq 35 \mu\text{m}$ in length)	<i>K. virgatodecaisneana</i>
36b	Carpogonia long ( $\geq 35 \mu\text{m}$ in length)	36
37a	Carposporophytes lower than whorls, $\leq 170 \mu\text{m}$ in height	<i>K. abilii</i>
37b	Carposporophytes higher than whorls, $\geq 240 \mu\text{m}$ in height	<i>K. celesbes</i>
38a	Carposporophytes loose	<i>K. faroensis</i>
38b	Carposporophytes dense	39
39a	Carpogonia short ( $\leq 25 \mu\text{m}$ in length)	<i>K. novaecaledonensis</i>
39b	Carpogonia long ( $\geq 35 \mu\text{m}$ in length)	40
40a	Carposporangia large ( $\geq 17 \mu\text{m}$ in length, $\geq 11 \mu\text{m}$ in diameter), known distribution in Australasia	<i>K. gudjewga</i>
40b	Carposporangia small ( $\leq 17.5 \mu\text{m}$ in length, $\leq 10.5 \mu\text{m}$ in diameter), known distribution in North and South America	<i>K. ambigua</i>

***Kumanoa abilii*** (Reis) Necchi and ML Vis, *Phycologia* 49:101 (2010)  
(Fig. 5.21a–d)

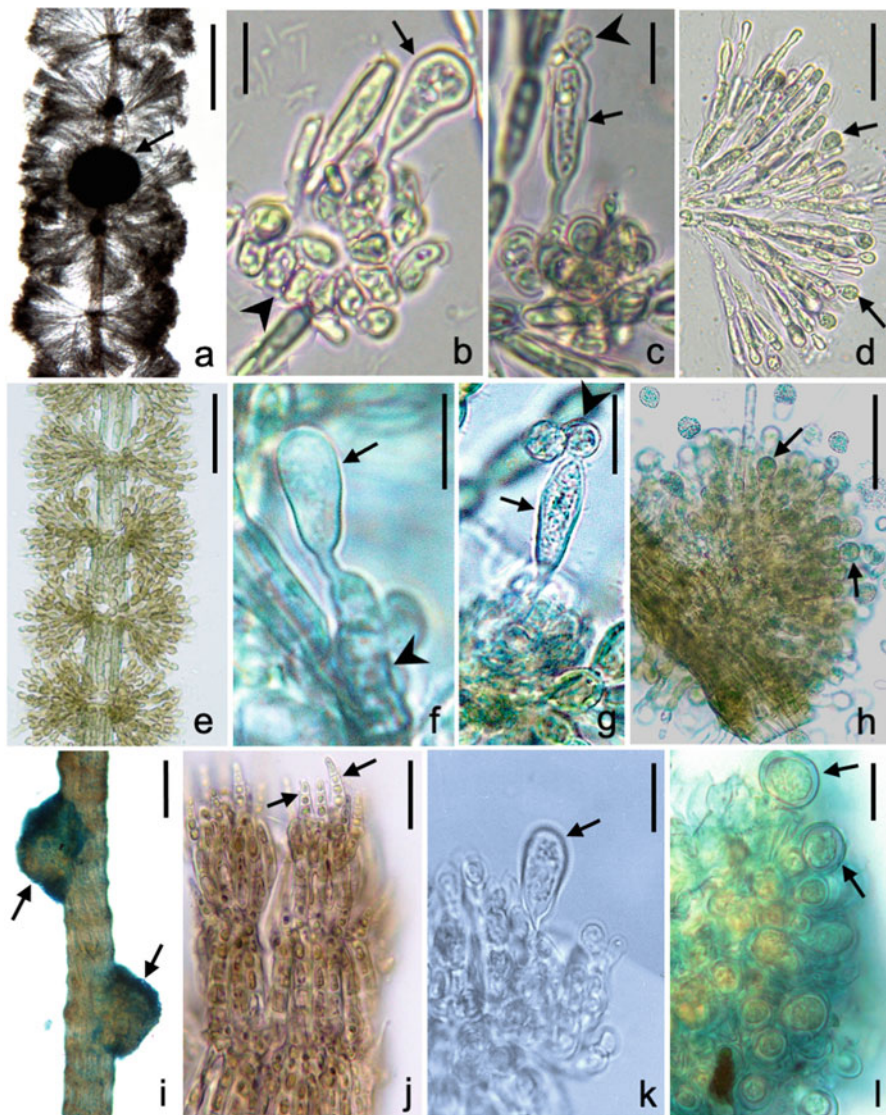
**Basionym:** *Batrachospermum abilii* Reis, *Bol Soc Brot* 39:138 (1965).

**Type:** COI, MP Reis and A Nauwerck 135, 28.iii.1960 (Holotype).

**Type locality:** Portugal, Beira Litoral Province, Vermoim River, near Oliveira de Azeméis, 41.242500° N, 08.604444° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, separated or contiguous, obconical, pear-shaped, barrel-shaped or spherical, 250–500  $\mu\text{m}$  in diameter; primary fascicles straight, 7–12 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal, obovoidal, or pear-shaped; secondary fascicles abundant, covering two-thirds to the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, 4–6  $\mu\text{m}$  in diameter; carpogonial branches straight or curved, rarely slightly helically twisted, arising from pericentral or proximal fascicle cells, rarely on secondary fascicles or intercalary cells of carpogonial branches, composed of 2–8 disc- or barrel-shaped cells; carpogonia 30–60  $\mu\text{m}$  in length with sessile or stalked, cylindrical, clavate, elongate-ellipsoidal or bottle-shaped trichogynes, 6–9  $\mu\text{m}$  in diameter; carposporophytes 1, rarely 2 per whorl, dense, lower than the whorls, 150–400  $\mu\text{m}$  in diameter, 80–170  $\mu\text{m}$  in height; gonimoblast filaments with 3–6 cylindrical or ellipsoidal cells; carposporangia obovoidal, 12.0–19.0  $\mu\text{m}$  in length, 7.5–12.0  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to other two species of *Kumanoa* (*K. spermatiophora* and *K. virgatodecaisneana*) by having straight or curved, rarely slightly helically twisted carpogonial branches, but differs by the presence



**Fig. 5.21** (a–d) *Kumanoa abili*: (a) well-developed whorls with dense carposporophyte (arrow); (b) carpogonium with clavate trichogyne (arrow) and curved carpogonial branch (arrowhead); (c) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa alakaiensis*: (e) reduced whorls; (f) young carpogonium with clavate trichogyne (arrow) and twisted carpogonial branch (arrowhead); (g) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (h) dense carposporophyte with carposporangia (arrows); (i–l) *Kumanoa amazonensis*: (i) reduced and compact whorls with carposporophytes (arrows); (j) compact whorls with short primary fascicles (arrows); (k) carpogonium with clavate trichogyne (arrow); (l) dense carposporophyte with carposporangia (arrows). Scale bars: (a) = 500  $\mu\text{m}$ ; (e, i) 100  $\mu\text{m}$ ; (b, c, f–g, k, l) = 10  $\mu\text{m}$ ; (d) = 25  $\mu\text{m}$ ; (h, j) = 50  $\mu\text{m}$  (Image author: (e–h) AR Sherwood)

of spermatangia on ordinary fascicle cells, longer carpogonia ( $\geq 35$   $\mu\text{m}$  in length), and shorter carpogonial branches ( $\leq 8$  cells).

**Representative sequences in GenBank:** JN604915 (COI-5P); GQ368882, GQ368883 (*rbcL*).

**Distribution:** Europe: Portugal; South America: Brazil (Fig. 5.16).

**Key references:** Reis (1965b), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa alakaiensis* AR Sherwood, CA Jones, and KY Conklin, Pac Sci 68:579 (2014) (Fig. 5.21e–h)

**Type:** BISH 754835, CA Jones, and AR Sherwood, 25.iii.2013 (Holotype); US 217950, US 217951 (Isotypes).

**Type locality:** the USA, Hawaii, Kauai, Kōke'e State Park, Kawaikōi Stream at crossing of Alaka'i Swamp Trail, 22.146733° N, 159.613450° W.

**Description:** thalli monoecious; branching irregular; whorls reduced, separated or contiguous, sub-spherical or obconical, 95–155  $\mu\text{m}$  in diameter; primary fascicles curved, (4–)5–7(–8) cells, proximal cells cylindrical or barrel-shaped, distal cells ellipsoidal or barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 4–6  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells or proximal fascicle cells, composed of 8–10 disc-shaped cells; carpogonia 20–30  $\mu\text{m}$  in length with sessile or stalked and clavate trichogynes, 6.0–7.5  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, usually higher than whorls, 85–175  $\mu\text{m}$  in diameter, 75–125  $\mu\text{m}$  in height; gonimoblast filaments with 4–6 barrel-shaped cells; carposporangia spherical or obovoidal, 10–17  $\mu\text{m}$  in length, 8.5–12.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species most closely resembles two others with reduced whorls (*K. amazonensis* and *K. gibberosa*), but differs in the following combination of characters: irregular branching, discernable whorls in most parts of the thalli, non-audouinelloid primary fascicle cells, abundant secondary fascicles.

**Representative sequences in GenBank:** KF042065 (COI-5P); KF042064 (*rbcL*).

**Distribution:** Pacific Islands: Hawaii (Fig. 5.16).

**Key reference:** Sherwood et al. (2014).

*Kumanoa amazonensis* Necchi and ML Vis, Phycologia 49:99 (2010) (Fig. 5.21i–l)

**Type:** SP 400148, D Pascoaloto, 01.xii.1999 (Holotype).

**Type locality:** Brazil, Amazonas State, Manaus, Route AM-10, km 25, “Adolfo Ducke” Forest Reserve, Acará Stream, 02.951667° S, 59.950278° W.

**Description:** thalli monoecious; branching irregular; whorls reduced, dense and compact, usually indistinct, separated, 100–150  $\mu\text{m}$  in diameter; primary fascicles audouinelloid, curved, unilaterally branches, 3–6(–7) cells, proximal cells cylindrical, distal cells cylindrical or barrel-shaped; secondary fascicles absent; spermatangia obovoidal or sub-spherical, on primary fascicles, 4.5–6.5  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising on pericentral or

proximal fascicle cells, composed of 4–6 disc or barrel-shaped cells; carpogonia 20–30  $\mu\text{m}$  in length with sessile and clavate trichogynes, 7–9  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, semi-spherical, higher than the whorls, 140–220  $\mu\text{m}$  in diameter, 80–130  $\mu\text{m}$  in height; gonimoblast filaments with 3–7 cylindrical or barrel-shaped cells; carposporangia obovoidal or sub-spherical, 11–14  $\mu\text{m}$  in length, 7.5–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to *K. gibberosa* in vegetative morphology, having extremely reduced and dense whorls with a cartilaginous consistency, but differs in lacking secondary fascicles.

**Representative sequences in GenBank:** JN604916 (COI-5P); GQ368884 (*rbcl*).

**Distribution:** South America: Brazil (Fig. 5.16).

**Key references:** Necchi et al. (2010), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa ambigua* (Montagne) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.22a–d)

**Basionym:** *Batrachospermum ambiguum* Montagne, *Ann Sci Nat, Bot*, ser 3, 14: 296 (1850).

**Type:** PC0738382, FMR Leprieur no. 1110 (Lectotype here designated, Isolectotypes PC).

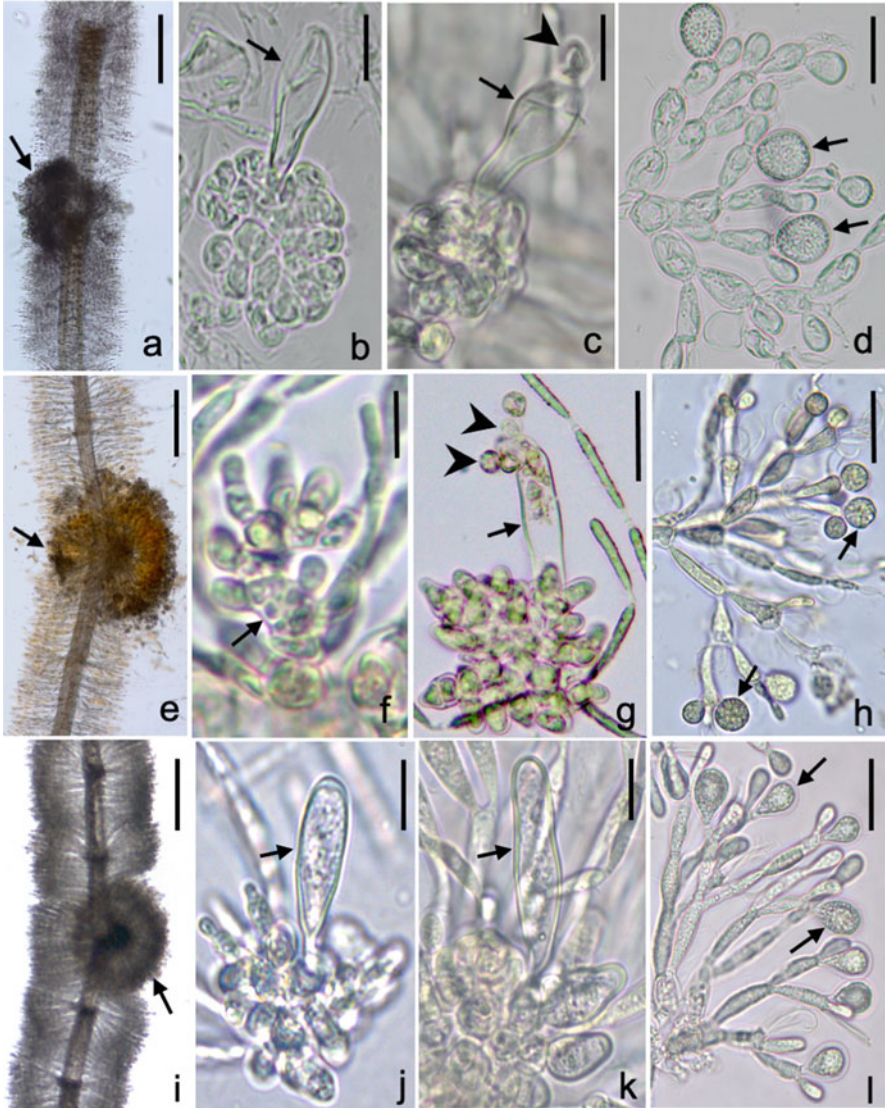
**Type locality:** French Guiana, Rivulet Orapu, locality not specified, 4.510880° N, 52.353630° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 275–600  $\mu\text{m}$  in diameter; primary fascicles straight, (6–)7–12(–15) cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal, obovoidal, or pear-shaped; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or sub-spherical, on primary or secondary fascicles, 5–7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral, rarely on proximal cells of primary fascicles, composed of 4–8 disc or barrel-shaped cells; carpogonia (15–)23–43(–65)  $\mu\text{m}$  in length, with sessile and cylindrical, clavate, ellipsoidal, or elongate-conical trichogynes, 6–10(–12.5)  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, lower or higher than whorls, 120–300(–450)  $\mu\text{m}$  in diameter, 90–200(–250)  $\mu\text{m}$  in height; gonimoblast filaments with 3–7 cylindrical or ellipsoidal cells; carposporangia obovoidal, 10–17.5  $\mu\text{m}$  in length, (5–)6.5–10.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from other species of *Kumanoa* by the following combination of characters: irregular branching, well-developed whorls with 7 or more cells composed of cylindrical, ellipsoidal, or obovoid fascicle cells, abundant secondary fascicles covering the entire internode, helically twisted and short ( $\leq 8$  cells) carpogonial branches, dense carposporophytes that are lower or higher than the whorl radius and obovoid, relatively small ( $\leq 17.5$   $\mu\text{m}$  in length,  $\leq 10.5$   $\mu\text{m}$  in diameter) carposporangia.

**Representative sequences in GenBank:** EU095970, JN604917 (COI-5P); AY423390, GQ368885 (*rbcl*).





**Fig. 5.22** (a–d) *Kumanoa ambigua*: (a) well-developed whorls with carposporophyte (arrow); (b) young twisted carpogonial branch (arrow); (c) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa americana*: (e) well-developed whorls with carposporophytes (arrow); (f) young twisted carpogonial branch (arrow); (g) mature carpogonium with clavate trichogyne (arrow); (h) gonimoblast filaments with carposporangia (arrows); (i–l) *Kumanoa australica*: (i) reduced whorls with carposporophytes (arrows); (j) young twisted carpogonial branch (arrows); (k) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (l) dense carposporophyte with carposporangia (arrows). Scale bars: (e, i) = 250 µm; (a) 100 µm; (d, h, l) = 25 µm; (b, c, f, g, j, k) = 10 µm



**Distribution:** North America: Belize, Costa Rica, and Puerto Rico; South America: Brazil, French Guiana (Fig. 5.16).

**Key references:** Sheath et al. (1992), Vis et al. (2004, 2005), Necchi and Vis (2012), Vis et al. (2012).

**Remarks:** Sheath et al. (1992) designated specimen PC0452179 as the holotype but it is not part of Montagne collection at PC presumably because they were unaware of the Montagne collection at the time. One of the syntypes (PC0738382) is here designated as lectotype since it is the one used by Montagne to describe the species.

*Kumanoa americana* (RG Sheath, ML Vis, and KM Cole) ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48:752 (2012) (Fig. 5.22e–h)

**Basionym:** *Batrachospermum procarpum* var. *americanum* RG Sheath, ML Vis, and KM Cole, J Phycol 28:244 (1992).

**Type:** UBC A8265, RG Sheath FL3, 29.xii.1986 (Holotype).

**Type locality:** the USA: Florida, Hillsborough County, Citrus Park, Brushy Creek at Gunn Road, 28.065833° N, 82.555000° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, contiguous, obconical, or barrel-shaped, 190–450 µm in diameter; primary fascicles audouinelloid, curved, unilaterally branched, 11–16 cells, proximal cells cylindrical, distal cells cylindrical or barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles, 5–7.5 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–9 disc- or barrel-shaped cells; carpogonia 19.0–35.0(–38.0) µm in length, with cylindrical or clavate, stalked or unstalked trichogynes, 5.5–10.5 µm in diameter; carposporophytes 1–2 per whorl, dense, lower than whorls, 90–240 µm in diameter, 55–130 µm in height; gonimoblast filaments with 3–6 cylindrical cells; carposporangia obovoidal or sub-spherical, 12–15 µm in length, 5.5–11 µm in diameter.

**Diagnostic characters:** this species most closely resembles *K. procarpa* in vegetative morphology (pseudodichotomous branching, well-developed whorls, audouinelloid primary fascicles, and secondary fascicles covering the entire internode), but differs by having longer primary fascicles, with ≥11 cells, shorter carpogonia (≤35 µm in length) and dense carposporophytes, which are lower than the whorls.

**Representative sequences in GenBank:** JN604910 (COI-5P); JN589995, JN589996 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.16).

**Key references:** Sheath et al. (1992), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa australica* (Entwisle and Foard) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.22i–l)

**Basionym:** *Batrachospermum australicum* Kützing ex Entwisle and Foard, Austral Syst Bot 12:624 (1999).

**Type:** DNA D0266493, TJ Entwisle 2709, 02.vi.1997 (Holotype); MEL 2045069A (Isotype).

**Type locality:** Australia, Northern Territory, Elsey Station, Roper River, 14.947671° S, 133.208554° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, 260–410 µm in diameter; primary fascicles straight, (6–)7–12 cells, proximal cells cylindrical, ellipsoidal or fusiform, distal cells ellipsoidal or fusiform; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, forming clusters, 4–6 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of (11–)15–21(–26) disc or barrel-shaped cells; carpogonia 30–50 µm in length, with sessile and clavate, cylindrical or fusiform trichogynes, 4–8 µm in diameter; carposporophytes 1–2 per whorl, dense, lower, rarely higher than whorls, 115–200 µm in diameter, 60–110 µm in height; gonimoblast filaments with 3–6 cylindrical or barrel-shaped cells; carposporangia obovoidal or ellipsoidal, 10–17 µm in length, 9–12 µm in diameter.

**Diagnostic characters:** this species differs from other species of the genus in having the unique spermatangia arranged in clusters; in addition, it has very long carpogonial branches (typically  $\geq 15$  cells).

**Representative sequences in GenBank:** EU636720 (COI-5P); FJ386463, JN589997 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.16).

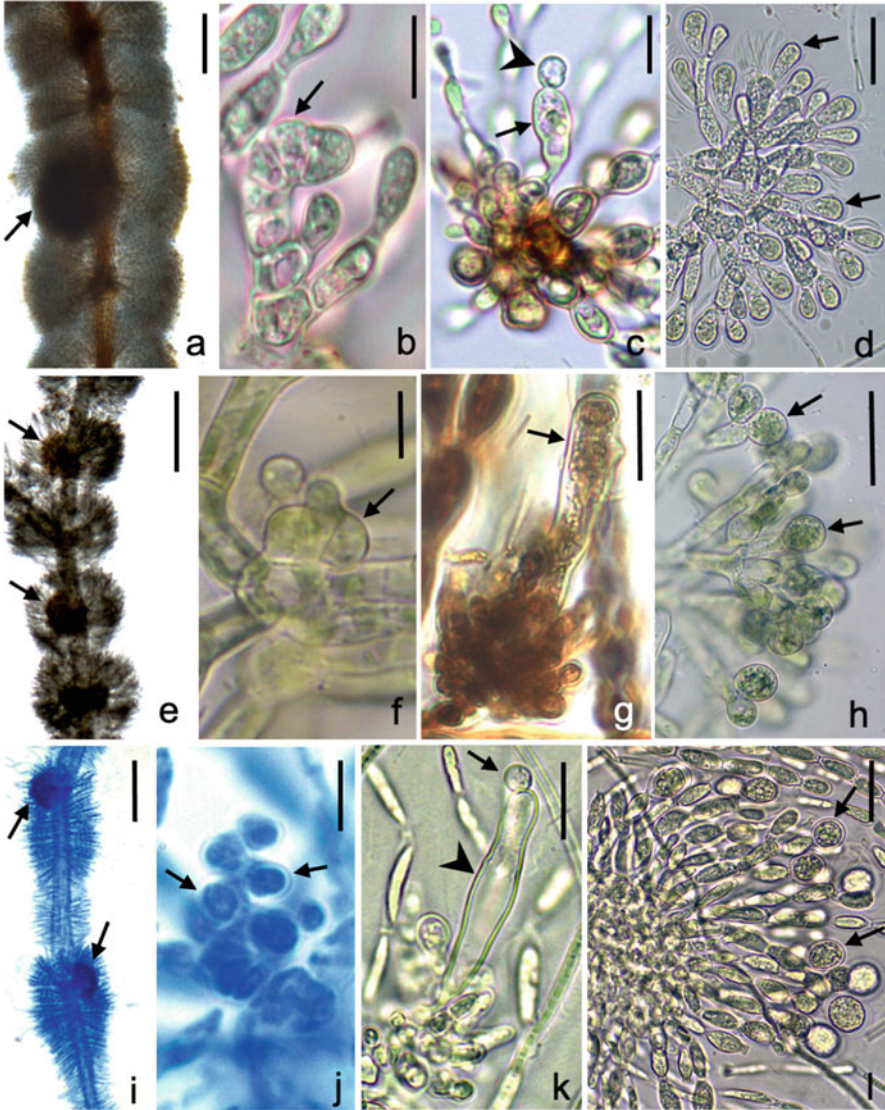
**Key references:** Entwisle and Foard (1999), Necchi and Vis (2012), Vis et al. (2012).

***Kumanoa bouwmanii*** AL Szinte, JC Taylor, and ML Vis, *Phycologia* 59:194 (2020) (Fig. 5.23a–d)

**Type:** SANDC 19–564, JC Taylor, 01.vi.2012 (Holotype); BHO A-0950 (Isotype).

**Type locality:** Zambia, Lufubu River at Chipili Village, M13 road-bridge, North-Western Zambia, 10.728889° S, 29.094444° E.

**Description:** thalli monoecious; branching irregular; whorls reduced, separated or contiguous, elongate-obconical, 260–320 µm in diameter; primary fascicles straight, 5–8 cells, proximal and distal cells cylindrical or ellipsoidal; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 5–8 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 3–5 disc- or barrel-shaped cells; carpogonia 24–40(–50) µm in length with sessile and clavate trichogynes, 9–12(–15) µm in diameter; carposporophytes 1–2 per whorl, dense, as high as or higher than whorls, 255–300 µm in diameter, 103–150 µm in height; gonimoblast filaments with 3–5 barrel-shaped or ellipsoidal cells; carposporangia sub-spherical, 16–28 µm in length, 12–24 µm in diameter.



**Fig. 5.23** (a–d) *Kumanoa bouwmanii*: (a) reduced whorls with dense carposporophyte (arrow); (b) mature carpogonium with clavate trichogyne (arrow); (c) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa capensis*: (e) reduced whorls with loose carposporophyte (arrow); (f) young coiled carpogonial branch (arrow); (g) fertilized carpogonium with cylindrical trichogyne (arrow) and attached spermatia (arrowheads); (h) gonimoblast filaments with carposporangia (arrows); (i–l) *Kumanoa celebes*: (i) well-developed whorls with loose carposporophyte (arrow); (j, k) mature carpogonia with ellipsoidal trichogynes (arrows); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (a, e, i) = 250 µm; (d, h, l) = 25 µm; (b, c, f, g, j, k) = 10 µm

**Diagnostic characters:** this species is morphologically similar to *K. nodiflora* in having reduced and elongate-obconical whorls but differs for having irregular branching and larger and sub-spherical carposporangia ( $\geq 16 \mu\text{m}$  in length,  $\geq 12 \mu\text{m}$  in diameter) in contrast to pseudodichotomous branching and obovoidal or ellipsoidal and smaller carposporangia ( $15\text{--}20 \mu\text{m}$  in length,  $10\text{--}13 \mu\text{m}$  in diameter) in *K. nodiflora*. In addition, *K. nodiflora* is only known from South America (French Guiana) and DNA sequence data are divergent (3.4% for *rbcL* and 5.9% for COI-5P).

**Representative sequences in GenBank:** MN974521 (COI-5P); MN974516 (*rbcL*).

**Distribution:** Africa: Zambia (Fig. 5.16).

**Key reference:** Szinte et al. (2020).

*Kumanoa capensis* (Starmach ex Kumano and Necchi) Necchi and ML Vis, Phycologia 49:101 (2010) (Fig. 5.23e–h)

**Basionym:** *Batrachospermum capense* Starmach ex Kumano and Necchi, Jap J Phycol 32:349 (1984).

**Type:** KRA, J Rzoska, 1972 (Lectotype, designated by Necchi and Kumano 1984); SP187186 (Isolectotype).

**Type locality:** Seychelles, Mahé Island, Du Cap River,  $4.681944^\circ \text{S}$ ,  $55.480556^\circ \text{E}$ .

**Description:** thalli monoecious or dioecious; branching irregular; whorls reduced or well developed, contiguous, obconical,  $300\text{--}1000 \mu\text{m}$  in diameter; primary fascicles straight,  $4\text{--}12(\text{--}15)$  cells, proximal cells fusiform, ellipsoidal or elongate-cylindrical, distal cells fusiform or ellipsoidal; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles,  $5.5\text{--}7.5 \mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells or proximal fascicle cells, composed of  $5\text{--}9$  disc or barrel-shaped cells; carpogonia  $40\text{--}85 \mu\text{m}$  in length, with sessile or stalked and cylindrical, clavate or elongate-ellipsoidal trichogynes,  $7\text{--}9 \mu\text{m}$  in diameter; carposporophytes 1 per whorl, loose, higher or lower than whorls,  $350\text{--}850 \mu\text{m}$  in diameter,  $190\text{--}400 \mu\text{m}$  in height; gonimoblast filaments with  $5\text{--}10$  cylindrical or elongate-ellipsoidal cells; carposporangia obovoidal or spherical,  $10.5\text{--}16 \mu\text{m}$  in length,  $8\text{--}12 \mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from other species of *Kumanoa* in having primary fascicles with thin and elongate cells (fusiform, ellipsoidal or elongate-cylindrical), loose carposporophytes, and carposporangia obovoidal or spherical, relatively small.

**Representative sequences in GenBank:** JX504695, JX504696 (COI-5P); JX504697, JX504698 (*rbcL*).

**Distribution:** Africa: Seychelles; South America: Brazil; French Guiana (Fig. 5.16).

**Key references:** Necchi and Kumano (1984), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa celebes* ET Johnston, N Buhari and ML Vis, *Phycologia* 53:335 (2014) (Fig. 5.23i–l)

**Type:** MICH 1229174, E Johnston, N Buhari, F Saint Amour, 09.viii.2011 (Holotype); BHO A-1000 (Isotype).

**Type locality:** Indonesia, Central Sulawesi, Bomba Valley, Sungai Tomehipi near Kolori Village, 01.475000° S, 120.189167° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 425–575 µm in diameter; primary fascicles straight, 9–13 cells, proximal cells cylindrical or ellipsoidal, distal cells obovoidal or pear-shaped; secondary fascicles abundant covering the entire internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 5.5–7 µm in diameter; carpogonial branches curved or slightly helically twisted, arising from the pericentral cells, composed of 3–7 disc- or barrel-shaped cells; carpogonia 40–51 µm with sessile and clavate or ellipsoidal trichogynes, 7.5–11 µm in diameter; carposporophytes 1 per whorl, dense, higher or as high as whorls, 315–420 µm in diameter and 240–390 µm in height; gonimoblast filaments with 3–5 cylindrical or ellipsoidal cells; carposporangia obovoidal, 15–20 µm in length, 11–12 µm in diameter.

**Diagnostic characters:** this species differs from other species of *Kumanoa* occurring in Southeast Asia by the following combination of characters: well-developed whorls, with non-audouinelloid primary fascicles, 9–13 cells, curved or slightly helically twisted carpogonial branches, dense carposporophytes that are usually higher than whorls and obovoidal and long carposporangia ( $\geq 15$  µm in length).

**Representative sequences in GenBank:** KF557551 (*rbcL*).

**Distribution:** Asia: Indonesia (Fig. 5.16).

**Key reference:** Johnston et al. (2014).

*Kumanoa cipoensis* (Kumano and Necchi) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.24a–d)

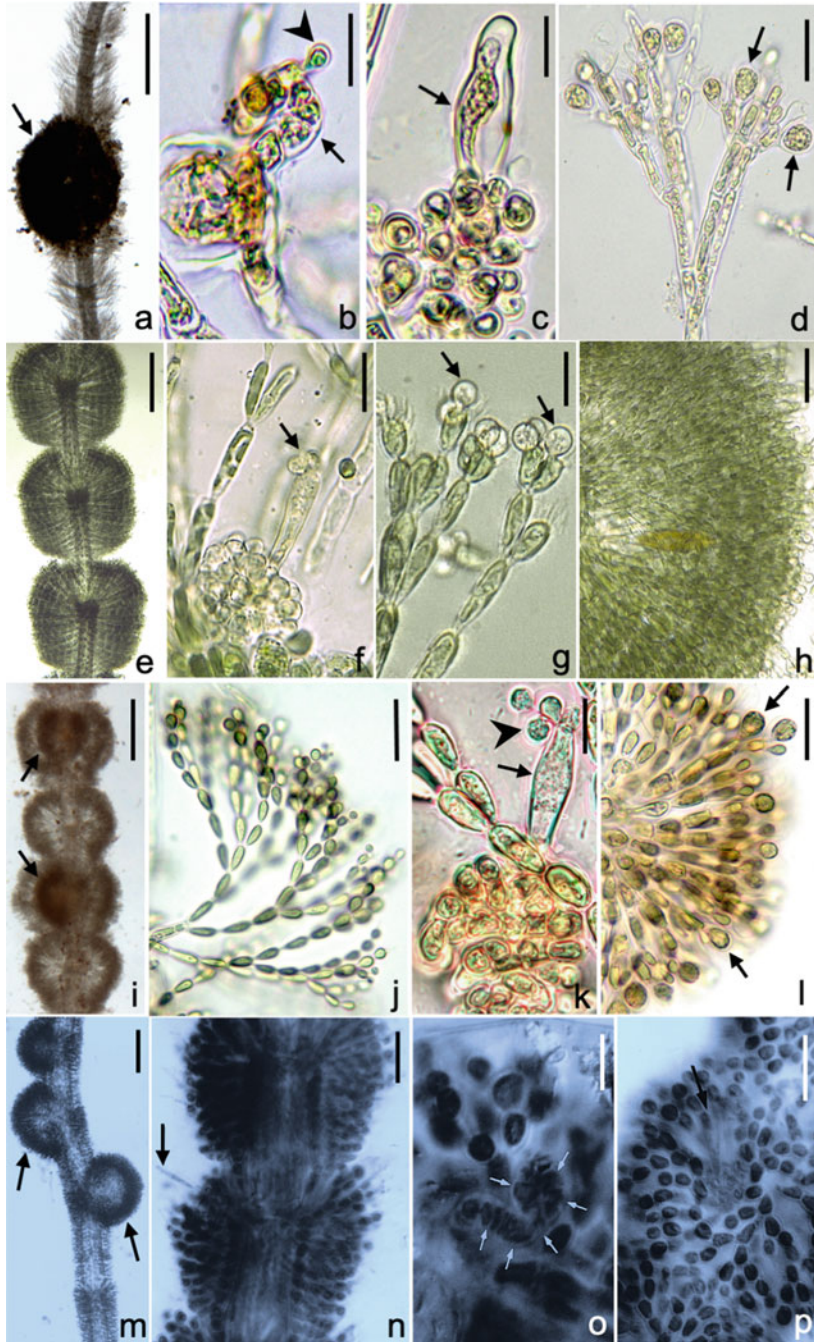
**Basionym:** *Batrachospermum cipoense* Kumano and Necchi, *Jap J Phycol* 33: 183 (1985).

**Type:** SP, L Sormus 408, 07.ii.1976 (Holotype).

**Type locality:** Brazil, Minas Gerais State, Serra do Cipó National Park, Serra do Cipó, 19.348611° S, 43.545833° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, contiguous, obconical, 350–700 µm in diameter; primary fascicles audouinelloid, curved, mostly unilaterally branched, 12–20 cells, proximal cylindrical, distal cells cylindrical or barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles, rarely on involucre filaments, 5–8 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–10 disc or barrel-shaped cells; carpogonia 35–50 µm in length, with sessile and clavate or ellipsoidal trichogynes, 7–10 µm in diameter; carposporophytes 1 per whorl, dense, higher than whorls, 350–800 µm in diameter, 250–500 µm in





**Fig. 5.24** (a–d) *Kumanoa cipoensis*: (a) well-developed whorls with dense carposporophyte (arrow); (b) young coiled carposogonial branch (arrow) with developing trichogyne (arrowhead); (c) mature carposogonium with ellipsoidal trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa comperei*: (e) reduced whorls; (f) fertilized carposogonium; (g) gonimoblast filaments; (h) dense carposporophyte; (i–l) *Kumanoa* sp.: (i) whorls; (j) gonimoblast filaments; (k) carposporangia; (l) carposporangia; (m–p) *Kumanoa* sp.: (m) whorls; (n) whorls; (o) carposporangia; (p) carposporangia.



height; gonimoblast filaments with 7–10 cylindrical cells; carposporangia obovoidal or sub-spherical, 13–19  $\mu\text{m}$  in length, 10–17  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to other species having pseudodichotomous branching and audouinelloid primary fascicles (*K. americana*, *K. equisetoides*, *K. procarpa*, and *K. tiomanensis*) but differs by this combination of characters: primary fascicles  $\geq 12$  cells, abundant secondary fascicles, large and dense carposporophytes, that are higher than whorls.

**Representative sequences in GenBank:** JN604918, JN604919 (COI-5P); GQ368887, GQ368888 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.17).

**Key references:** Kumano and Necchi (1985), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa comperei* E Fischer, D Killmann, and D Quandt, *Pl Fung Syst* 65:153 (2020) (Fig. 5.24e–h)

**Type:** BR, RW Fischer 294/17 (AC 039), 23.iii.2017 (Holotype); KOBL (Isotype).

**Type locality:** Rwanda, Western Province, Nyungwe National Park, stream in montane forest S of Kamiranzovu Swamp, along main road RN6, 2.485872° S, 29.165381° E.

**Description:** thalli monoecious; branching irregular; whorls reduced, contiguous or separated, barrel-shaped or obconical, 155–390  $\mu\text{m}$  in diameter; primary fascicles straight, with 6–8 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia spherical, 5–6  $\mu\text{m}$  in diameter, on primary and secondary fascicles; carpogonial branches helically twisted, arising from pericentral cells, composed of 4–6 cells; carpogonia 25–35  $\mu\text{m}$  in length, with sessile and clavate trichogynes, 9–11  $\mu\text{m}$  in diameter; carposporophytes 1(–2) per whorl, usually higher than whorls, dense, 270–300  $\mu\text{m}$  in diameter, 210–250  $\mu\text{m}$  in height; gonimoblast filaments 6–8 cells; carposporangia obovoidal or ellipsoidal, 5–7 in length, 4–5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is mostly closely related phylogenetically (Fig. 5.20) and geographically (Fig. 5.16, 5.17) to *K. bouwmanii* but *K. comperei* differs by the presence of thicker distal fascicle cells (length/

**Fig. 5.24** (continued) with clavate trichogyne and attached spermatia (*arrow*); (**g**) primary fascicles with terminal spermatangia (*arrows*); (**h**) carposporophyte; (**i–l**) *Kumanoa curvata*: (**i**) well-developed whorls with dense carposporophytes (*arrows*); (**j**) curved primary fascicles; (**k**) fertilized carpogonium with ellipsoidal trichogyne (*arrow*) and attached spermatia (*arrowhead*); (**l**) gonimoblast filaments with carposporangia (*arrows*); (**m–p**) *Kumanoa deminuta*: (**m**) reduced whorls with dense carposporophytes (*arrows*); (**n**) reduced whorl with fusiform trichogyne (*arrow*); (**o**) young coiled carpogonial branch (*arrows*); (**p**) mature carpogonium with clavate trichogyne (*arrow*). *Scale bars:* (**a**) = 500  $\mu\text{m}$ ; (**i**) = 250  $\mu\text{m}$ ; (**e, m**) = 100  $\mu\text{m}$ ; (**j, l**) = 50  $\mu\text{m}$ ; (**d, h, l, n, p**) = 25  $\mu\text{m}$ ; (**b, c, f, g, k, o**) = 10  $\mu\text{m}$  (Image author: Fig. (e–h) E Fischer. Fig. (m–p) reprinted with permission by the publisher (CSIRO) from Entwisle and Foard (1999))

diameter < 2.5) that are ellipsoidal or obovoidal, as well as obovoidal or ellipsoidal and smaller carposporangia ( $\leq 7 \mu\text{m}$  in length,  $\leq 5 \mu\text{m}$  in diameter); in contrast *K. bouwmanii* has thinner distal cells (length/diameter >2.5) that are elongate-ellipsoidal or fusiform, and spherical and larger carposporangia ( $\geq 16 \mu\text{m}$  in length,  $\geq 12 \mu\text{m}$  in diameter).

**Representative sequences in GenBank** MT109270 (COI-5P); MT109256, MT109260 (*rbcL*).

**Distribution:** Africa: Democratic Republic of the Congo, Rwanda (Fig. 5.17).

**Key reference:** Fischer et al. (2020).

*Kumanoa curvata* (Shi) ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48: 756 (2012) (Fig. 5.24i–l)

**Basionym:** *Batrachospermum curvatum* Shi, Acta Phytotax Sin 32:275 (1994).

**Type:** HP, Zhi-Xin Shi, 15.vi.1981 (Holotype).

**Type locality:** China, Hubei, Yuquansi in Dangyang Xian, 30.780556° N, 111.703056° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, or pear-shaped, 250–400  $\mu\text{m}$  in diameter; primary fascicles curved, 6–12 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal, obovoidal, or sub-spherical; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, 4.5–6.5  $\mu\text{m}$  in diameter; carpogonial branches curved or slightly helically twisted, arising from pericentral cells, composed of 4–7 disc- or barrel-shaped cells; carpogonia 25–35  $\mu\text{m}$  in length, with sessile or stalked and cylindrical, clavate or ellipsoidal trichogynes, 6–9  $\mu\text{m}$  in diameter; carposporophytes 1 (–2) per whorl, dense, lower, or less often higher than whorls, 80–300  $\mu\text{m}$  in diameter, 60–150  $\mu\text{m}$  in height; gonimoblast filaments with 5–8 cylindrical or ellipsoidal cells; carposporangia obovoidal or pear-shaped, 13–18  $\mu\text{m}$  in length, 10–14  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species most closely resembles *K. iriomotensis* in vegetative morphology (well-developed whorls, non-audouinelloid primary fascicles with  $\geq 6$  cells) but differs by the presence of curved primary fascicles and carpogonial branches that are curved or slightly helically twisted.

**Representative sequences in GenBank:** JN604925 (COI-5P); JN590012 (*rbcL*).

**Distribution:** Asia: China; South America: Brazil (Fig. 5.17).

**Key references:** Shi (1994), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa deminuta* (Entwisle and Foard) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.24m–p)

**Basionym:** *Batrachospermum deminutum* Entwisle and Foard, Austral Syst Bot 12: 627 (1999).

**Type:** NSW, TJ Entwisle 2638, 24.vii.1996 (Holotype); MEL 2043857A, MEL 2278402A (Isotypes).

**Type locality:** Australia, New South Wales, 2.5 km NE of Kurradjong, Mill Road crossing, Little Wheeny Creek, 33.558333° S, 150.685000° E.

**Description:** thalli monoecious; branching irregular; whorls reduced, contiguous, obconical or elongate-obconical, 100–160 µm in diameter; primary fascicles curved, 4–7 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 5–6.5 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 11–19 disc- or barrel-shaped cells; carpogonia 34–39 µm in length, with sessile and clavate, ellipsoidal, or fusiform trichogynes, 4–8 µm in diameter; carposporophytes 1–2 per whorl, dense, higher than whorls, 150–230 µm in diameter, 80–150 µm in height; gonimoblast filaments with 4–9 cylindrical or barrel-shaped cells; carposporangia sub-spherical or obovoidal, 7–13 µm in length, 7–11 µm in diameter.

**Diagnostic characters:** this species is similar to several other species of *Kumanoa* with reduced whorls but differs by the following combination of characters: irregular branching, non-audouinelloid primary fascicles, long carpogonial branches ( $\geq 11$  cells), and small carposporangia ( $\leq 13$  µm in length,  $\leq 11$  µm in diameter).

**Representative sequences in GenBank:** EU636721 (COI-5P); AF209981 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.17).

**Key references:** Entwisle and Foard (1999), Necchi and Vis (2012), Vis et al. (2012).

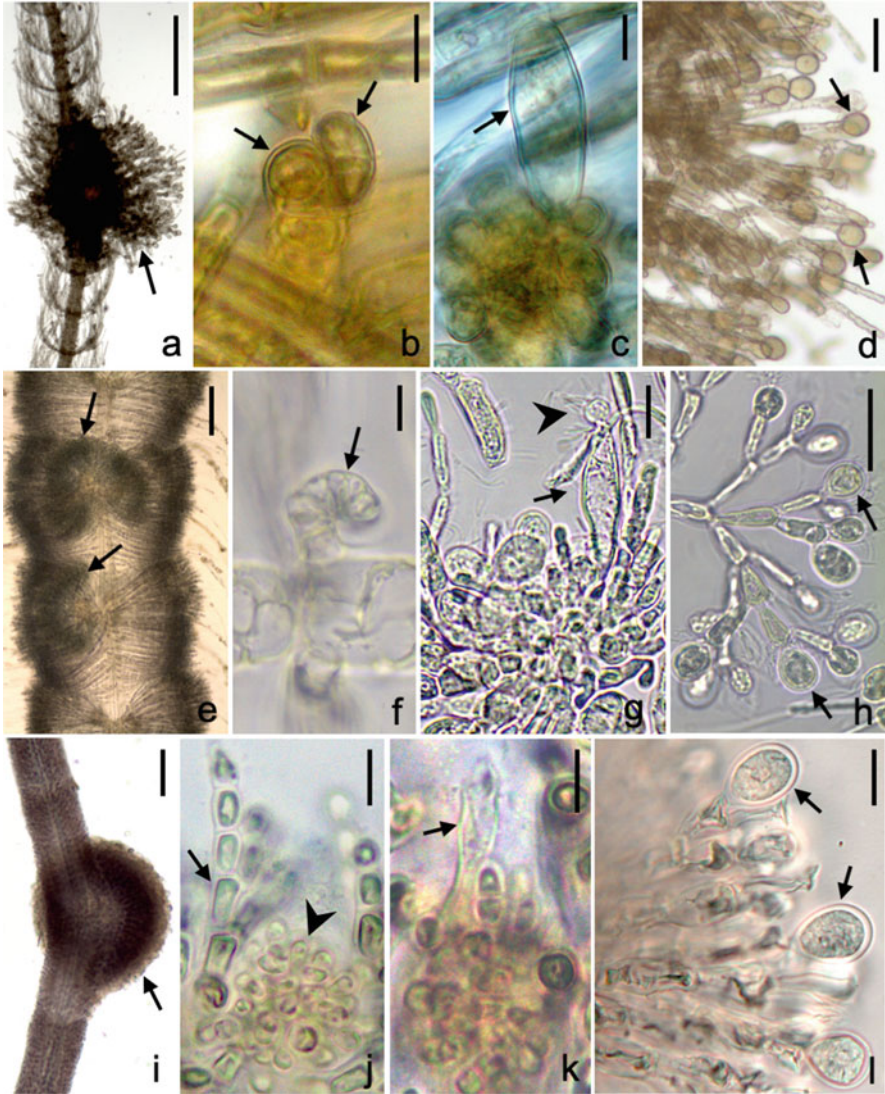
*Kumanoa equisetoides* (Kumano and Necchi) Entwisle, ML Vis, WB Chiasson, Necchi and A R Sherwood, J Phycol 45:710 (2009) (Fig. 5.25a–d)

**Basionym:** *Batrachospermum equisetoides* Kumano and Necchi, Jap J Phycol 33: 182 (1985).

**Type:** SP, O Necchi Jr, 31.i.1984 (Holotype).

**Type locality:** Brazil, Amazonas State, Manaus, “Adolfo Ducke” Forest Reserve, Acará Stream, 02.951667° S, 59.950278° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, separated, barrel-shaped, 400–800 µm in diameter; primary fascicles audouinelloid, curved, 10–16 cells, proximal and distal cells cylindrical; secondary fascicles absent or few and sparse; spermatangia spherical or obovoidal, on primary, rarely on secondary fascicles, 6–9 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–8 disc- or barrel-shaped cells; carpogonia 40–55 µm in length, with sessile or stalked and cylindrical or ellipsoidal trichogynes, 10–13 µm in diameter; carposporophytes 1 per whorl, loose, higher than whorls, 500–850 µm in diameter, 300–600 µm in height; gonimoblast filaments with 7–10 cylindrical cells; carposporangia spherical or sub-spherical, 20–32 µm in length, 17–27 µm in diameter.



**Fig. 5.25** (a–d) *Kumanoa equisetoides*: (a) well-developed whorls with loose carposporophyte (arrow); (b) young coiled carpogonial branch (arrows); (c) mature carpogonium with ellipsoidal trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa faroensis*: (e) well-developed whorls with loose carposporophytes (arrows); (f) young coiled carpogonial branch (arrow); (g) fertilized carpogonium with ellipsoidal trichogyne (arrow) and attached spermatium (arrowhead); (h) gonimoblast filaments with carposporangia (arrows); (i–l) *Kumanoa gibberosa*: (i) reduced and compact whorls with dense carposporophyte (arrow); (j) young coiled carpogonial branch (arrow); (k) mature carpogonium with clavate trichogyne (arrow); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (a) = 500 µm; (e, i) = 100 µm; (d) = 50 µm; (h) = 25 µm; (b, c, f, g, j–l) = 10 µm

**Diagnostic characters:** this species is similar to other species having pseudodichotomous branching and audouinelloid primary fascicles (*K. americana*, *K. procarpa*, and *K. tiomanensis*) but differs by this combination of characters: primary fascicles  $\geq 10$  cells, lack of secondary fascicles, large and loose carposporophytes, that are higher than whorls, larger carposporangia ( $\geq 20 \mu\text{m}$  in length,  $\geq 17 \mu\text{m}$  in diameter).

**Representative sequences in GenBank:** EU636716 (COI-5P); GQ368889, GQ368890 (*rbcL*).

**Distribution:** South America: Brazil, Venezuela (Fig. 5.17).

**Key references:** Kumano and Necchi (1985), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa faroensis* (Kumano and WA Bowden-Kerby) ML Vis, Necchi, WB Chiasson and Entwisle, J Phycol 48:756 (2012) (Fig. 5.25e–h)

**Basionym:** *Batrachospermum faroense* Kumano and WA Bowden-Kerby, Jap J Phycol 34:123 (1986).

**Type:** TNS-AL, WA Bowden-Kerby, 11.v.1982 (Holotype).

**Type locality:** Micronesia, Caroline Islands, Truk, Tol Island, Faro Village, 07.326325° S, 151.627637° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 300–600  $\mu\text{m}$  in diameter; primary fascicles straight, 7–12(–14) cells, proximal cells ellipsoidal or cylindrical, distal cells obovoidal, pear-shaped, or sub-spherical; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 4–7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–11(–14) disc- or barrel-shaped cells; carpogonia 30–45(–52)  $\mu\text{m}$  in length, with sessile and clavate or ellipsoidal trichogynes, 5–12  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, loose, lower than whorls, 200–320  $\mu\text{m}$  in diameter, 120–200  $\mu\text{m}$  in height; gonimoblast filaments with 4–6 cylindrical or barrel-shaped cells; carposporangia obovoidal or sub-spherical, 10–16.5  $\mu\text{m}$  in length, 7–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to *K. spermatiphora* in vegetative (well-developed whorls, straight primary fascicles composed of cylindrical, ellipsoidal, or obovoid fascicle cells) and reproductive morphology (long carpogonial branches  $\leq 12$  cells, loose carposporophytes that are lower than whorls), but differs by lacking specialized spermatangial branches (spermatiphores) and also in having abundant secondary fascicles, helically twisted carpogonial branches and smaller carposporophytes ( $\leq 320 \mu\text{m}$  in diameter,  $\leq 200 \mu\text{m}$  in height).

**Representative sequences in GenBank:** JN604907 (COI-5P); JN590001 (*rbcL*).

**Distribution:** North America: the USA; Pacific Islands: Micronesia (Fig. 5.17).

**Key references:** Kumano and Bowden-Kerby (1986), Necchi and Vis (2012), Vis et al. (2012).



***Kumanoa gibberosa*** (Kumano) Necchi and ML Vis, *Phycologia* 49:101 (2010) (Fig. 5.25i–l)

**Basionym:** *Tuomeya gibberosa* Kumano, *Bot. Mag. Tokyo* 91:105 (1978).

**Type:** TNS-AL, S Kumano, 12.ix.1971 (Holotype).

**Type locality:** Malaysia, Negeri Sembilan, Pasoh Forest Reserve, Sungai Maron Kanan, 02.870833° N, 102.254722° E.

**Description:** thalli monoecious; branching pseudodichotomous; whorls reduced, compact, contiguous, obconical, 70–170 µm in diameter; primary fascicles densely arranged, curved, unilaterally branched, 3–6(–7) cells, proximal and distal cells short-cylindrical to barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical to sub-spherical, on secondary, less often on primary fascicles, 4–7 µm in diameter; carpogonial branches on pericentral cells, composed of 4–10 disc- or barrel-shaped cells; carpogonia 25–35 µm in length with sessile and cylindrical to clavate trichogynes, 4–6 µm in diameter; carposporophytes 1 per whorl, dense, higher than whorls, 100–370 µm in diameter, 70–170 µm in height; gonimoblast filaments with 5–8 cylindrical or barrel-shaped cells; carposporangia spherical or sub-spherical, less often obovoidal, 10–15 µm in length, 7–15 µm in diameter.

**Diagnostic characters:** this species is similar to *K. amazonensis* in having reduced and compact whorls but differs by the presence of abundant secondary fascicles, covering the entire internode.

**Representative sequences in GenBank:** KF557552 (*rbcL*).

**Distribution:** Asia: Malaysia; South America: Brazil (Fig. 5.17).

**Key references:** Kumano (1978), Necchi and Vis (2012), Vis et al. (2012).

***Kumanoa globospora*** (Israelson) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.26a–d)

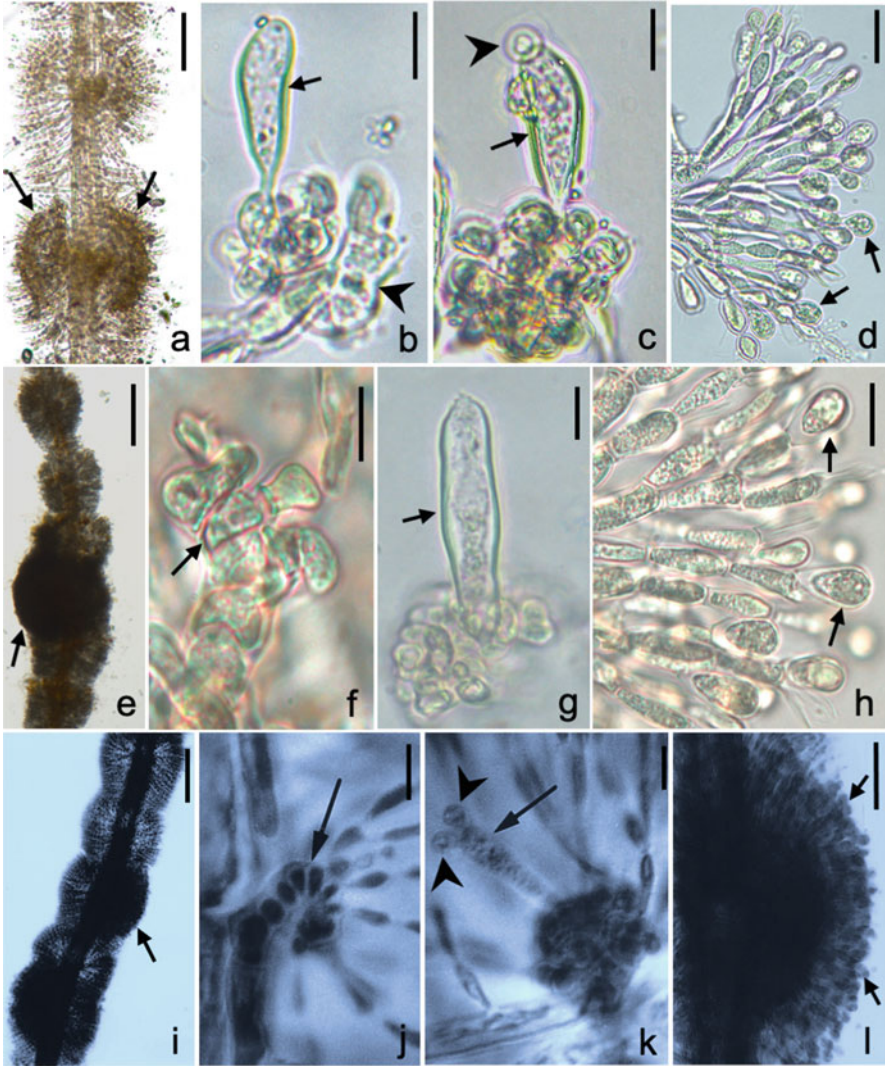
**Basionym:** *Batrachospermum globosporum* Israelson, *Symb Bot Upsal* 6: 44 (1942).

**Type:** UPS:BOT:A-000174, G Lohammar, 5.x.1941 (Holotype).

**Type locality:** Sweden, Dalarna, Folkarna, Lake Asgarn, 60.258333° N, 16.248889° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, or barrel-shaped; 300–600 µm in diameter; primary fascicles straight, 7–12 cells, proximal cells ellipsoidal or fusiform, distal cells ellipsoidal or fusiform; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or obovoidal, on primary or secondary fascicles, 6–7.5 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 4–7 disc- or barrel-shaped cells; carpogonia 20–34(–40) µm in length with stalked or sessile and cylindrical, ellipsoidal, or clavate trichogynes, 4.5–9.5(–12.0) µm in diameter; carposporophytes 1 per whorl, loose, lower than the whorls, (160–)200–350(–420) µm in diameter, (80–)100–200(–305) µm in height; gonimoblast filaments with 4–8 cylindrical





**Fig. 5.26** (a–d) *Kumanoa globospora*: (a) well-developed whorls with loose carposporophytes (arrows); (b) mature carpogonium with clavate trichogyne (arrow); (c) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa gracillima* (e) well-developed whorls with dense carposporophyte (arrow); (f) young coiled carpogonial branch (arrow); (g) fertilized carpogonium with ellipsoidal trichogyne (arrow) and attached spermatium (arrowhead); (h) gonimoblast filaments with carposporangia (arrows); (i–l) *Kumanoa gudjewga*: (i) well-developed whorls with dense carposporophyte (arrow); (j) young coiled carpogonial branch (arrow); (k) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatia (arrowheads); (l) dense carposporophyte with carposporangia (arrows). Scale bars: (e, i) = 250  $\mu\text{m}$ ; (a) = 100  $\mu\text{m}$ ; (l) = 50  $\mu\text{m}$ ; (d) = 25  $\mu\text{m}$ ; (b, c, f–h, j, k) = 10  $\mu\text{m}$  (Fig. (i–l) reprinted with permission from Entwisle and Foard (1999))

or ellipsoidal cells; carposporangia sub-spherical or obovoidal, 9–13(–15)  $\mu\text{m}$  in length, 6–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species can be distinguished from other species of *Kumanoa* by the following combination of characters: well-developed whorls, straight primary fascicles composed of thin and elongate cells (ellipsoidal or fusiform), abundant secondary fascicles, short carpogonial branches ( $\leq 7$  cells), loose carposporophytes that are lower than whorls, small carposporophytes ( $\leq 350$   $\mu\text{m}$  in diameter,  $\leq 200$   $\mu\text{m}$  in height), and carposporangia ( $\leq 13$   $\mu\text{m}$  in length,  $\leq 11$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** JN604923 (COI-5P); GQ368891 (*rbcL*).

**Distribution:** Australasia: Australia; Europe: Sweden; North America: Belize, Mexico, the USA; South America: Brazil (Fig. 5.17).

**Key references:** Israelson (1942), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa gracillima* (W West and GS West emend. Necchi) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.26e–h)

**Basionym:** *Batrachospermum gracillimum* W West and GS West emend. Necchi, Bolm Bot 11:43 (1989).

**Type:** LISU, F Welwitsch 3.v.1857 (Lectotype); BM (Isotype).

**Type locality:** Angola, Pungo Andongo, River Tanque, 09.665833° S, 15.560833° E.

**Description:** thalli monoecious, rarely dioecious; branching irregular; whorls reduced, rarely well developed, contiguous, obconical, 200–500  $\mu\text{m}$  in diameter; primary fascicles straight, 4–9(–11) cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia spherical or sub-spherical, mainly on secondary fascicles and less often on primary fascicles, 5.7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–8 disc or barrel-shaped cells; carpogonia (35–)45–85  $\mu\text{m}$  in length with stalked or sessile and cylindrical or clavate trichogynes, 6–10  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, higher than the whorls, 200–470  $\mu\text{m}$  in diameter, 110–230  $\mu\text{m}$  in height; gonimoblast filaments with 5–9 cylindrical or elongate-ellipsoidal cells; carposporangia obovoidal, 12–17  $\mu\text{m}$  in length, 8–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from species with reduced whorls in having primary fascicles with cylindrical, ellipsoidal, or obovoid cells, spermatangia occurring mainly on secondary fascicles, carposporophytes that are dense and higher than the whorls and obovoidal and relatively small ( $\leq 17$   $\mu\text{m}$  in length,  $\leq 12$   $\mu\text{m}$  in diameter) carposporangia.

**Representative sequences in GenBank:** JN604913, JN604927 (COI-5P); AY423395 (*rbcL*).

**Distribution:** South America: Brazil, French Guiana; Africa: Angola (Fig. 5.17).

**Key references:** Necchi (1990), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa gudjewga* ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48:753 (2012)

**Type:** NSW 770937, TJ Entwisle 3370, 3.vii.2008 (Holotype) (Fig. 5.26i–l)

**Type locality:** Australia, Northern Territory, Kakadu National Park, tributary of Burdulba Creek, end of Gubara Walk, off Kakadu Highway, between Cooida and Jabiru, Gubara Pool, 12.795833° S, 132.794444° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, or barrel-shaped, 230–650 µm in diameter; primary fascicles straight, (6–)8–13(–15) cells; proximal cells cylindrical, ellipsoidal, or fusiform; distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 5–8 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–10 disc- or barrel-shaped cells; carpogonia 18–33(–48) µm in length, with sessile and clavate, obovoidal or ellipsoidal trichogynes, 6–9(–13) µm in diameter; carposporophytes 1 per whorl, dense, lower, or higher than whorls, 150–410(–600) µm in diameter, 75–210(–300) µm in height; gonimoblast filaments 3–6 cylindrical or barrel-shaped cells; carposporangia obovoidal, (14–)17–26 µm in length, (8–)11–17 µm in diameter.

**Diagnostic characters:** this species is similar to *K. ambigua* in most vegetative and reproductive characters but differs in having larger carposporangia ( $\geq 17$  µm in length,  $\geq 11$  µm in diameter). In addition, it is clearly separated by DNA sequences of COI-5P and *rbcL* genes and geographic distribution (restricted to Australia), whereas *K. ambigua* occurs in North and South America.

**Representative sequences in GenBank:** JN604908, JN604909 (COI-5P); JN590002, JN590003 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.17).

**Key references:** Entwisle and Foard (1999), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa henriquesiana* (Reis) Necchi and ML Vis, Bibliotheca Phycol 116:40 (2012)

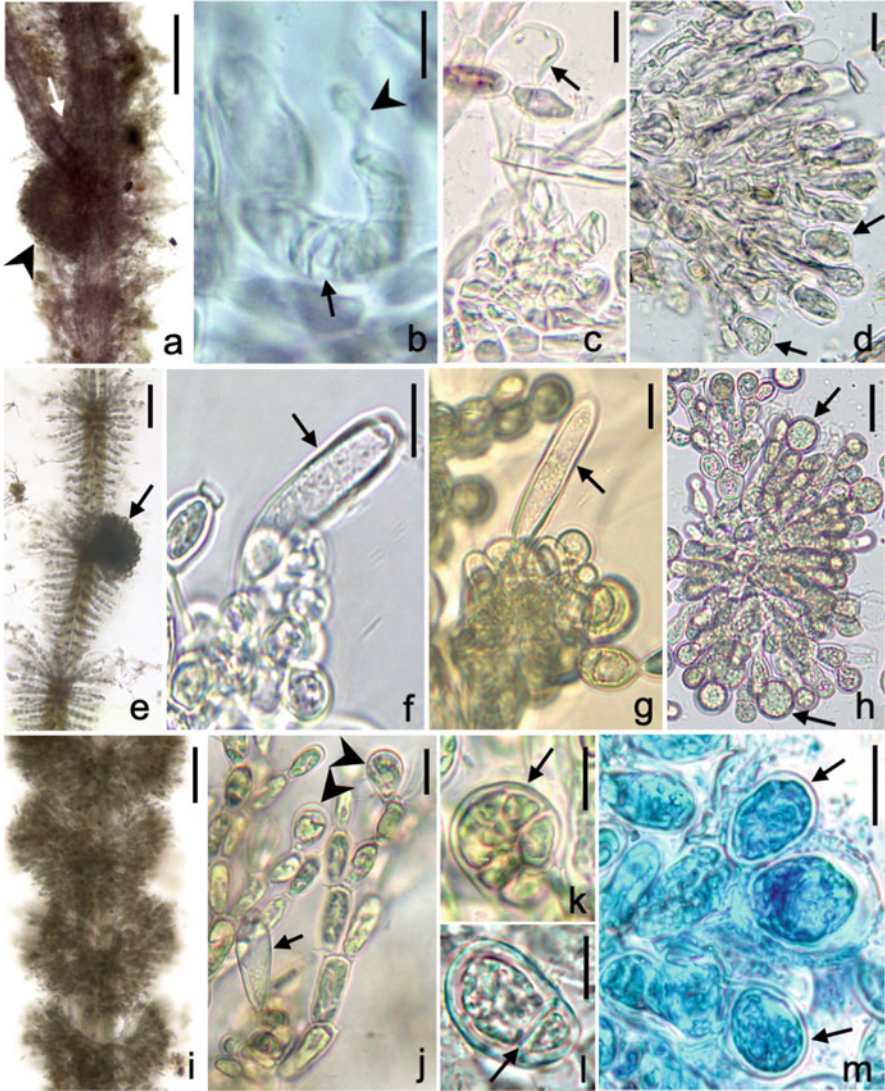
**Basionym:** *Batrachospermum henriquesianum* Reis, Bol Soc Brot 46:181 (1972a) (Fig. 5.27a–d)

**Type:** COI, MP Reis, and R Ferreira 566, 01.viii.1968 (Holotype).

**Type locality:** Portugal, Beira Litoral, Fonte Velha de Eirol, near Aveiro, 40.689722° N, 08.196944° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical or barrel-shaped, 250–400 µm in diameter; primary fascicles curved, 4–8 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 6.5–8.5 µm in diameter; carpogonial branches curved, slightly helically twisted, arising from pericentral cells, composed of 6–10 disc- or barrel-shaped cells; carpogonia 35–45 µm in length, with sessile and clavate trichogynes, 8–11 µm in diameter; carposporophytes 1 per whorl, dense, higher than the whorls,





**Fig. 5.27** (a–d) *Kumanoa henriquesiana*: (a) reduced whorls with pseudodichotomous branching (arrow) and dense carposporophyte (arrowhead); (b) young coiled carpogonial branch (arrow) with developing trichogyne (arrowhead); (c) mature carpogonium with clavate trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa holtonii*: (e) reduced whorls dense carposporophyte (arrow); (f, g) mature carpogonia with elongate-ellipsoidal trichogyne (arrows); (h) gonimoblast filaments with carposporangia (arrows); (i–m) *Kumanoa intorta*: (i) well-developed whorls; (j) primary fascicle showing carpogonium with clavate trichogyne at the base (arrow) and monosporangia at the tips (arrowheads); (k) young coiled carpogonial branch (arrow); (l) Bisporangium with a septum (arrow) dividing unequal parts; (m) gonimoblast filaments with carposporangia (arrows). Scale bars: (a) = 150  $\mu\text{m}$ ; (e, i) = 100  $\mu\text{m}$ ; (h) = 25  $\mu\text{m}$ ; (b–d, f, g, j–m) = 10  $\mu\text{m}$

150–300 µm in diameter, 100–180 µm in height; gonimoblast filaments with 4–7 cylindrical cells; carposporangia obovoidal or ellipsoidal, 18–25 µm in length, 10.5–15 µm in diameter.

**Diagnostic characters:** this species is similar to some species with straight or curved, rarely slightly helically twisted carpogonial branches (*K. abilii*, *K. louisianae*, *K. spermatiphora*, and *K. virgatodecaisneana*), but differs in having pseudodichotomous branching, reduced whorls and curved primary fascicles with  $\leq 8$  cells, dense carposporophytes that are higher than the whorl radius and large carposporangia ( $\geq 18$  µm in length).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Portugal (Fig. 5.17).

**Key references:** Reis (1972a), Necchi and Vis (2012).

*Kumanoa holtonii* ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48:753 (2012) (Fig. 5.27e–h)

**Type:** MICH 660537, K Goodman, 5.v.2009 (Holotype); BHO A-0234 (Isotype).

**Type locality:** the USA, Alabama, Tuscaloosa County, Cripple Creek, 33.492778° N, 87.562500° W.

**Description:** thalli monoecious; branching irregular; whorls reduced, contiguous, obconical, or pear-shaped, 200–300 µm in diameter; primary fascicles straight, 4–7 cells, proximal cells ellipsoidal or obovoidal, distal cells obovoidal or sub-spherical; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or sub-spherical, on primary or secondary fascicles, 5.5–7 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 4–7 disc- or barrel-shaped cells; carpogonia 42–55 µm in length with sessile, cylindrical, or elongate-ellipsoidal trichogynes, 8.0–10.5 µm in diameter; carposporophytes 1 per whorl, dense, higher than whorls, 110–270 µm in diameter, 100–170 µm in height; gonimoblast filaments with 3–5 cylindrical cells; carposporangia spherical or sub-spherical, 17–24 µm in length, 17–22.5 µm in diameter.

**Diagnostic characters:** this species is similar to some species with reduced whorls (*K. deminuta*, *K. louisianae*, *K. mahlacensis*, and *K. nodiflora*), but differs in having irregular branching, primary fascicles composed of ellipsoidal, obovoidal, or sub-spherical cells, abundant secondary fascicles covering the entire internode, helically twisted and short carpogonial branches ( $\leq 7$  cells), carposporophytes that are dense and higher than whorls and spherical or sub-spherical and large carposporangia ( $\geq 17$  µm in length and diameter).

**Representative sequences in GenBank:** JN604921 (COI-5P); JN590004 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.18).

**Key references:** Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa intorta* (Jao) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.27i–m)

**Basionym:** *Batrachospermum intortum* Jao, Sinensia 11:259 (1941).

**Type:** SC, CC Jao 52622, 09.i.1940 (Holotype).

**Type locality:** China, Szechwan, Pa-hsien, near Lung-chü Sze, 33.341328° N, 104.646107° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, 300–600 µm in diameter; primary fascicles straight, 6–12 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; monosporangia arising from primary and secondary fascicles or involucrel filaments, obovoidal, 11–15 µm in length, 9–12 in diameter; spermatangia spherical or sub-spherical, on primary or secondary fascicles, (5–)7–9 µm in diameter; carpogonial branches helically twisted, arising from pericentral or proximal cells, composed of (6–) 8–11 disc- or barrel-shaped cells; carpogonia 30–40 µm in length with sessile and clavate trichogynes, 6–9 µm in diameter; carposporophytes 1 per whorl, dense, higher than whorls, 150–300 µm in diameter, 85–150 µm in height; gonimoblast filaments with 4–7 cylindrical cells; carposporangia obovoidal or ellipsoidal, two types: small, 11–15 µm in length, 8–11.5 µm in diameter; large, 17–25 µm in length, 11–15 µm in diameter; bisporangia occasionally formed on gonimoblast filaments or loosely attached, obovoidal with septum dividing the content into two unequal parts.

**Diagnostic characters:** this species differs from the others of the genus forming monosporangia (*K. lusitanica*, *K. pseudocarpa*, and *K. woitapensis*) in having short carpogonia ( $\leq 40$  µm in length), monosporangia arising mainly from primary and secondary fascicles, dense carposporophytes that are higher than the whorl radius and two types of carposporangia, small ( $\leq 15$  µm in length and  $\leq 11.5$  µm in diameter) and large ( $\geq 17$  µm in length,  $\geq 11$  µm in diameter).

**Representative sequences in GenBank:** EU636717 (COI-5P); AY423397 (*rbcL*).

**Distribution:** Asia: China (Fig. 5.18).

**Key references:** Jao (1941), Necchi and Vis (2012), Xie et al. (2020).

***Kumanoa iriomotensis*** (Kumano) ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48:756 (2012) (Fig. 5.28a–d)

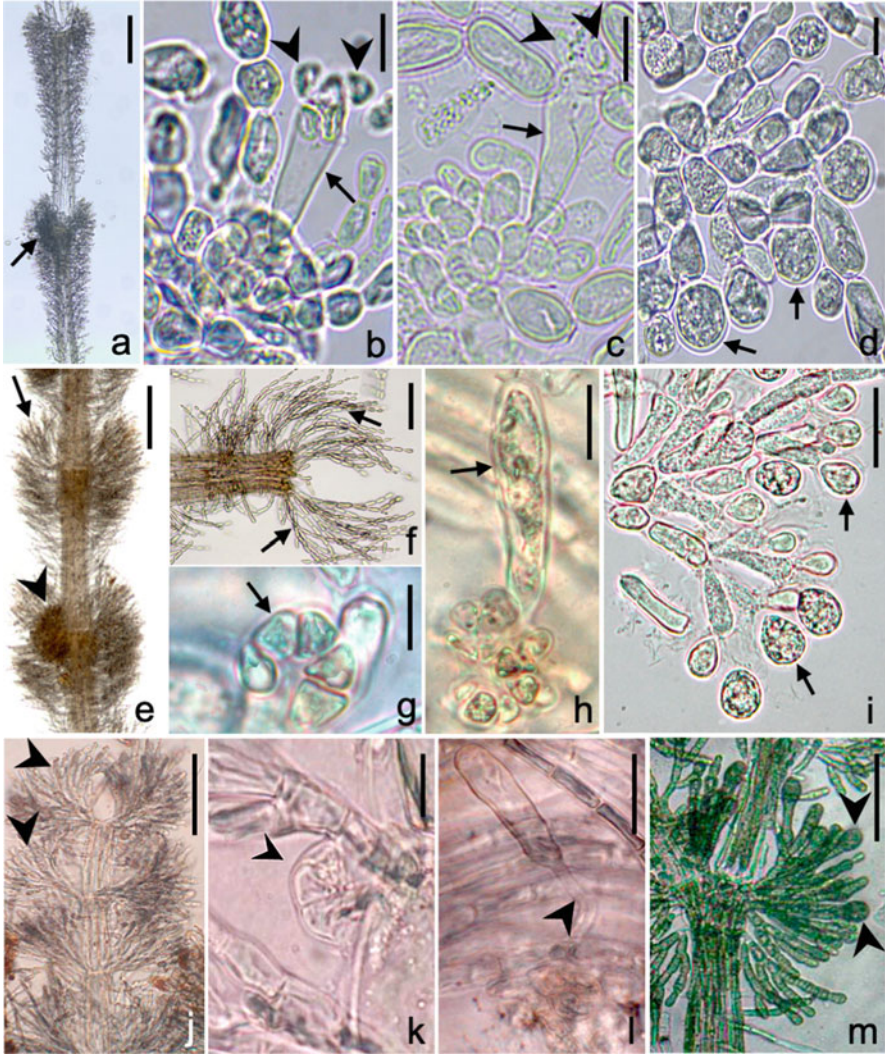
**Basionym:** *Batrachospermum iriomotense* Kumano, Jap J Phycol 30:182 (1982a).

**Type:** TNS-AL, Matsumoto, 23.iii.1974 (Holotype); SAP (Isotype).

**Type locality:** Japan, Okinawa, Iriomote Island, Sira-gawa River, 24.342341° N, 123.841898° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, separated, or contiguous, elongate-obconical or elongate-pear-shaped, 150–250 µm in diameter; primary fascicles straight, 8–10 cells, proximal cells fusiform, ellipsoidal or elongate-cylindrical, distal cells fusiform or ellipsoidal; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, 4–7 µm in diameter; carpogonial branches, helically twisted, arising from pericentral cells, composed of 8–12 disc- or barrel-shaped cells; carpogonia 26–40 µm in length with sessile and clavate trichogynes, 6.0–9.5 µm in diameter; carposporophytes 1 per whorl, dense, lower than the whorls, 100–220 µm in diameter, 70–150 µm in height;





**Fig. 5.28** (a–d) *Kumanoa iriomotensis*: (a) well-developed whorls with dense carposporophyte (arrow); (b, c) fertilized carpogonia with clavate trichogynes (arrows) and attached spermatia (arrowheads); (d) gonimoblast filaments with carposporangia (arrows); (e–i) *Kumanoa jolyi*: (e) well-developed whorls with curved primary fascicles (arrow) and dense carposporophyte (arrowhead); (f) whorl with curved primary fascicles (arrows); (g) young coiled carpogonial branch (arrow); (h) mature carpogonium with clavate trichogyne (arrow); (i) gonimoblast filaments with carposporangia (arrows); (j–m) *Kumanoa khaoluangensis*: (j) reduced whorls with audouinelloid primary fascicles (arrowheads); (k) young coiled carpogonial branch (arrowhead); (l) mature carpogonium with clavate trichogyne and stalked trichogyne (arrowhead); (m) loose carposporophyte with carposporangia (arrows). Scale bars: (e) = 250  $\mu\text{m}$ ; (a, f, j) = 100  $\mu\text{m}$ ; (m) = 50  $\mu\text{m}$ ; (i) = 25  $\mu\text{m}$ ; (b–d, g, h, k, l) = 10  $\mu\text{m}$  (Image author: (j–m) W Chankaew)

gonimoblast filaments with 4–6 cell cylindrical or barrel-shaped cells; carposporangia obovoidal or sub-spherical, 13–19  $\mu\text{m}$  in length, 11.5–14  $\mu\text{m}$  in diameter.

**Diagnostic features:** this species most closely resembles *K. mahlacensis* and *K. nodiflora* in vegetative morphology (elongate and obconical whorls) but differs in having the following combination of characters: well-developed whorls with fascicles  $\geq 8$  cells, carposporophytes lower than whorls and large carposporangia ( $\geq 13$   $\mu\text{m}$  in length,  $\geq 11.5$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** JN590011 (*rbcL*).

**Distribution:** Africa: South Africa; Asia: Japan, Malaysia (Fig. 5.18).

**Key references:** Kumano (1982), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa jolyi* (Necchi) Necchi and ML Vis, Phycologia 49:101 (2010)  
(Fig. 5.28e–i)

**Basionym:** *Batrachospermum jolyi* Necchi, Rev Bras Biol 46:520 (1986).

**Type:** SP 131570, O Yano 408, 25.viii.1978 (Holotype).

**Type locality:** Brazil, São Paulo State, Cananéia, Cardoso Island, 25.134517° S, 47.923442° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous or separated, obconical, barrel-shaped, or spherical, 400–800  $\mu\text{m}$  in diameter; primary fascicles curved, 13–20 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, rarely on involucrel filaments, 5–7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, rarely on rhizoidal filaments, composed of 6–10 disc- or barrel-shaped cells; carpogonia 30–40  $\mu\text{m}$  in length with sessile and cylindrical or clavate trichogynes, 6–8  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, dense, lower than the whorls, 200–450  $\mu\text{m}$  in diameter, 100–250  $\mu\text{m}$  in height; gonimoblast filaments with 5–8 cylindrical cells; carposporangia obovoidal or sub-spherical, 10–14  $\mu\text{m}$  in length, 8–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species most closely resembles *K. skujana* in vegetative morphology (well-developed whorls, non-audouinelloid and curved primary fascicles  $\geq 13$  cells), but differs in having dense carposporophytes that are lower than whorls.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** South America: Brazil (Fig. 5.18).

**Key references:** Necchi (1986), Necchi and Vis (2012).

*Kumanoa khaoluangensis* (W Chankaew, Y Peerapornpisal and Kumano) Necchi and ML Vis, comb. nov. (Fig. 5.28j–m)

**Basionym:** *Batrachospermum khaoluangensis* W Chankaew, Y Peerapornpisal and Kumano, Chiang Mai J Sci 40:3 (2013).

**Type:** Walailak University Herbarium (not registered in Index Herbariorum), W Chankaew, 26.vi.2011 (Holotype).

**Type locality:** Thailand, Nakhon Si Thammarat Province, Lansaka District, Khao Kaeo Subdistrict, Huaycheesuk stream, 08.373889° N, 99.734722° E.

**Description:** thalli dioecious; branching irregular; whorls reduced, contiguous or separated, ellipsoidal, sub-spherical or barrel-shaped, 180–290 µm in diameter; primary fascicles audouinelloid, curved, unilaterally branched, 4–8 cells, proximal cells cylindrical, distal cells cylindrical or ellipsoidal; secondary fascicles lacking or sparse; spermatangia spherical, on primary fascicles, 2–4 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 3–5 disc- or barrel-shaped cells; carpogonia 34–40 µm in length with sessile or stalked and clavate or ellipsoidal trichogynes, 8–14 µm in diameter; carposporophyte 1 per whorl, loose, as high as or higher than whorls, 100–200 µm in diameter, 50–120 µm high, sometimes indistinguishable from whorls; gonimoblast filaments with 5–8 cylindrical or ellipsoidal cells; carposporangia obovoidal or sub-spherical, 16–20 µm in length, 10–14 µm in diameter.

**Diagnostic characters:** this species is distinct from all other species of *Kumanoa* by the following combination of characters: whorls reduced, primary fascicles curved, unilaterally branched, secondary fascicles lacking or sparse, carposporophytes loose (sometimes indistinguishable from whorls) and relatively large carposporangia ( $\geq 16$  µm in length,  $\geq 10$  µm in diameter).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Thailand (Fig. 5.18).

**Key reference:** Chankaew et al. (2013).

*Kumanoa louisianae* (Skuja) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.29a–d)

**Basionym:** *Batrachospermum louisianae* Skuja in Flint, Am J Bot: 36:549 (1949).

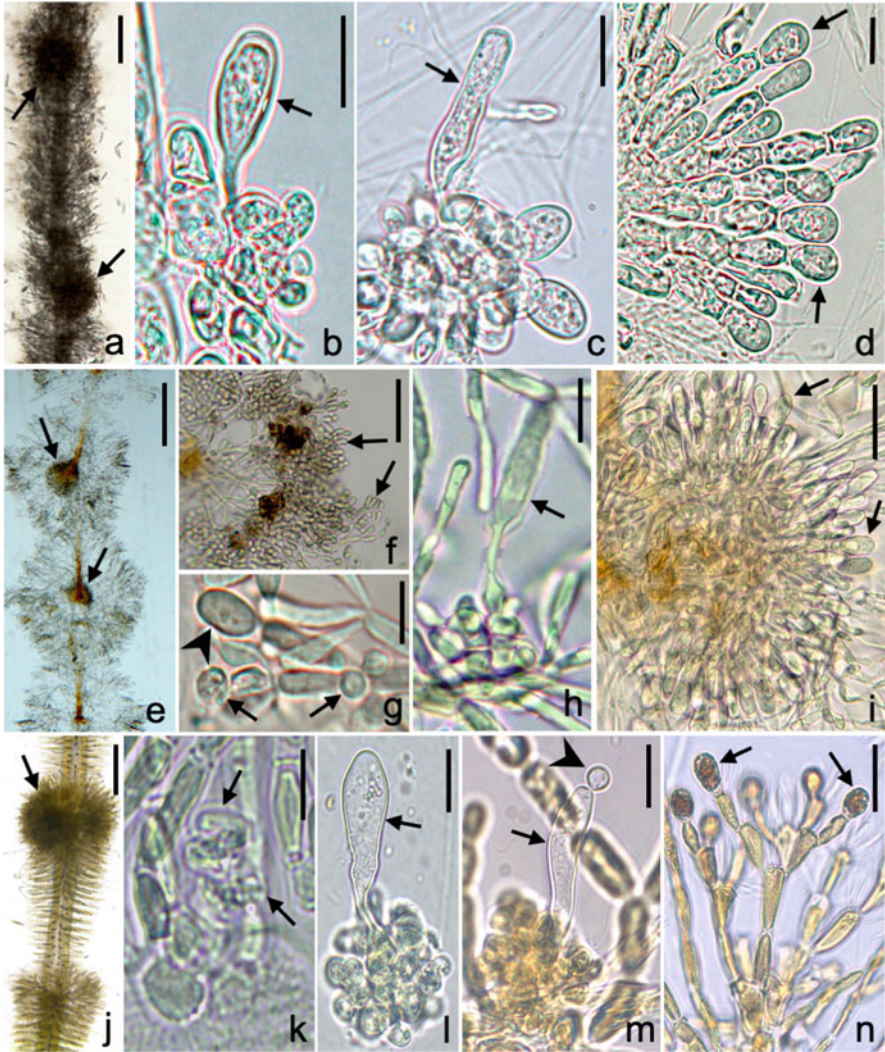
**Synonym:** *Kumanoa Hirosei* (Kumano and Ratnasabapathy) LM Liao, Philippine J Syst Biol 4:91 (2010).

**Type:** US 00312012, AB Langlois, 20.iv.1891 (Lectotype).

**Type locality:** the USA, Louisiana, Mandeville, 30.349444° N, 90.033056° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls reduced, contiguous, barrel-shaped, 250–410 µm in diameter; primary fascicles straight, 4–7(–9) cells, proximal cells elongate-ellipsoidal or elongate-cylindrical, distal cells ellipsoidal; secondary fascicles few to abundant, covering less than half of internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 5–7 µm in diameter; carpogonial branches curved, arising from pericentral cells, composed of 3–6 disc- or barrel-shaped cells; carpogonia 25.0–35.0 µm in length with stalked and clavate trichogynes, 6.0–11.5 µm in diameter; carposporophytes 1 per whorl, dense, lower than whorls, 150–250 µm in diameter, 80–175 µm in height; gonimoblast filaments with 3–5(–6) cylindrical





**Fig. 5.29** (a–d) *Kumanoa louisianae*: (a) reduced whorls with dense carposporophytes (arrows); (b) young carpogonium with stalked and clavate trichogyne (arrow); (c) mature carpogonium with clavate trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–i) *Kumanoa lusitanica*: (e) well-developed whorls with dense carposporophytes (arrows); (f) ring around a node with monosporangia (arrows); (g) primary fascicle with spermatangia (arrows) and monosporangium (arrowhead); (h) mature carpogonium with cylindrical trichogyne (arrow); (i) dense carposporophyte with carposporangia (arrows); (j–n) *Kumanoa mahlacensis*: (j) reduced whorls with dense carposporophyte (arrow); (k) young coiled carpogonial branch (arrows); (l) mature carpogonium with clavate trichogyne (arrow); (m) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (n) gonimoblast filaments with carposporangia (arrows). Scale bars: (e) = 250  $\mu\text{m}$ ; (a, j) = 150  $\mu\text{m}$ ; (f) = 100  $\mu\text{m}$ ; (i) = 50  $\mu\text{m}$ ; (g, n) = 25  $\mu\text{m}$ ; (b–d, h, k–m) = 10  $\mu\text{m}$

or ellipsoidal cells; carposporangia obovoidal or sub-spherical, 12–15  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to other species with reduced whorls, but differs by the following combination of characters: pseudodichotomous branching, barrel-shaped whorls with secondary fascicles covering less than half of the internode, carposporophytes that are dense and lower than whorls and relatively small carposporangia ( $\leq 15$   $\mu\text{m}$  in length,  $\leq 11$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** JN604924 (COI-5P); AF029144, JN590005 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.18).

**Key references:** Flint (1949), Sheath et al. (1992), Necchi and Vis (2012).

**Remarks:** Necchi and Vis (2012) listed *K. hirosei* as a doubtful species, possible synonym of *K. louisianae*, that is here formally proposed.

*Kumanoa lusitanica* (Reis) Necchi and ML Vis, Bibliotheca Phycol 116:49 (2012) (Fig. 5.29e–i)

**Basionym:** *Batrachospermum lusitanicum* Reis, Bol Soc Brot 39:141 (1965b).

**Type:** COI, MP Reis and A Santos 333, 18.v.1963 (Holotype).

**Type locality:** Portugal, Beira Alta, River Alfusqueiro, tributary of River Águeda, near Vouzela, 40.689722° N, 08.196944° W.

**Description:** thalli dioecious; branching irregular; whorls well-developed, contiguous, obconical or barrel-shaped, 350–650  $\mu\text{m}$  in diameter. Primary fascicles straight, 8–15 cells, proximal cells fusiform or ellipsoidal, distal cells fusiform or ellipsoidal; secondary fascicles abundant, covering the entire internode; monosporangia forming rings around the nodes on the axes, obovoidal, 20–26.5  $\mu\text{m}$  in length, 13–16 in diameter; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 6.5–8.5  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, rarely on secondary fascicles cortical filaments, composed of (6–)7–16 disc- or barrel-shaped cells; carpogonia 32.5–45  $\mu\text{m}$  in length with stalked or sessile and cylindrical or elongate-conical trichogynes, 8.0–10.5  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, dense, lower than whorls, 150–300  $\mu\text{m}$  in diameter, 90–150  $\mu\text{m}$  in height; gonimoblast filaments with 4–6 cylindrical cells; carposporangia ellipsoidal or elongate-obovoid, 20–23  $\mu\text{m}$  in length, 10–13.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from the others of the genus forming monosporangia (*K. intorta*, *K. pseudocarpa*, and *K. woitapensis*) in having rings of monosporangia on the nodes of axes, as well as long carpogonial branches (typically  $\geq 7$  cells), small carposporophytes ( $\leq 300$   $\mu\text{m}$  in diameter and  $\leq 150$   $\mu\text{m}$  in height) and long ( $\geq 20$   $\mu\text{m}$  in length) and ellipsoidal or elongate-obovoid carposporangia.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Portugal (Fig. 5.18).

**Key references:** Reis (1965b), Necchi and Vis (2012).

***Kumanoa mahlacensis*** (Kumano and WA Bowden-Kerby) ML Vis, Necchi, WB Chiasson, and Entwisle, *J Phycol* 48:756 (2012) (Fig. 5.29j–n)

**Basionym:** *Batrachospermum mahlacense* Kumano and WA Bowden-Kerby, *Jap J Phycol* 34:109 (1986).

**Type:** TNS-AL, WA Bowden-Kerby, 25.viii.1983 (Holotype).

**Type locality:** Micronesia, Mariana Islands, Guam, Talofoto, Mahlac River, upper reaches, 13.359444° N, 144.729581° E.

**Description:** thalli monoecious; branching irregular; whorls reduced, contiguous or separated, obconical or pear-shaped, 250–400 µm in diameter; primary fascicles straight, 4–7(–9) cells, proximal cells ellipsoidal or cylindrical, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 4–6 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of (5–)7–12(–15) disc- or barrel-shaped cells; carpogonia 25–40 µm in length with sessile and clavate or ellipsoidal trichogynes, 6–8 µm in diameter; carposporophytes 1–2 per whorl, dense, lower or less often higher than whorls, 140–180 µm in diameter, 75–160 µm in height; gonimoblast filaments with 4–6 cylindrical or barrel-shaped cells; carposporangia obovoidal or sub-spherical, 11–14 µm in length, 7–12 µm in diameter.

**Diagnostic features:** this species most closely resembles *K. iriomotensis* and *K. nodiflora* in vegetative morphology (elongate and obconical whorls), but differs in having the following combination of characters reduced whorls (primary fascicles  $\leq 7$  cells), carposporophytes typically lower than whorls and small carposporangia ( $\leq 14$  µm in length,  $\leq 12$  µm in diameter).

**Representative sequences in GenBank:** JN604906, MH220973 (COI-5P), JN590006, MH220972 (*rbcL*).

**Distribution:** Asia: China, Taiwan, and Thailand; Europe: Spain; North America: the USA; Pacific Islands: Micronesia (Fig. 5.18).

**Key references:** Kumano and Bowden-Kerby (1986), Necchi and Vis (2012), Vis et al. (2012), Garcia-Fernández et al. (2015), Xie et al. (2020).

***Kumanoa montagnei*** Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.30a–d)

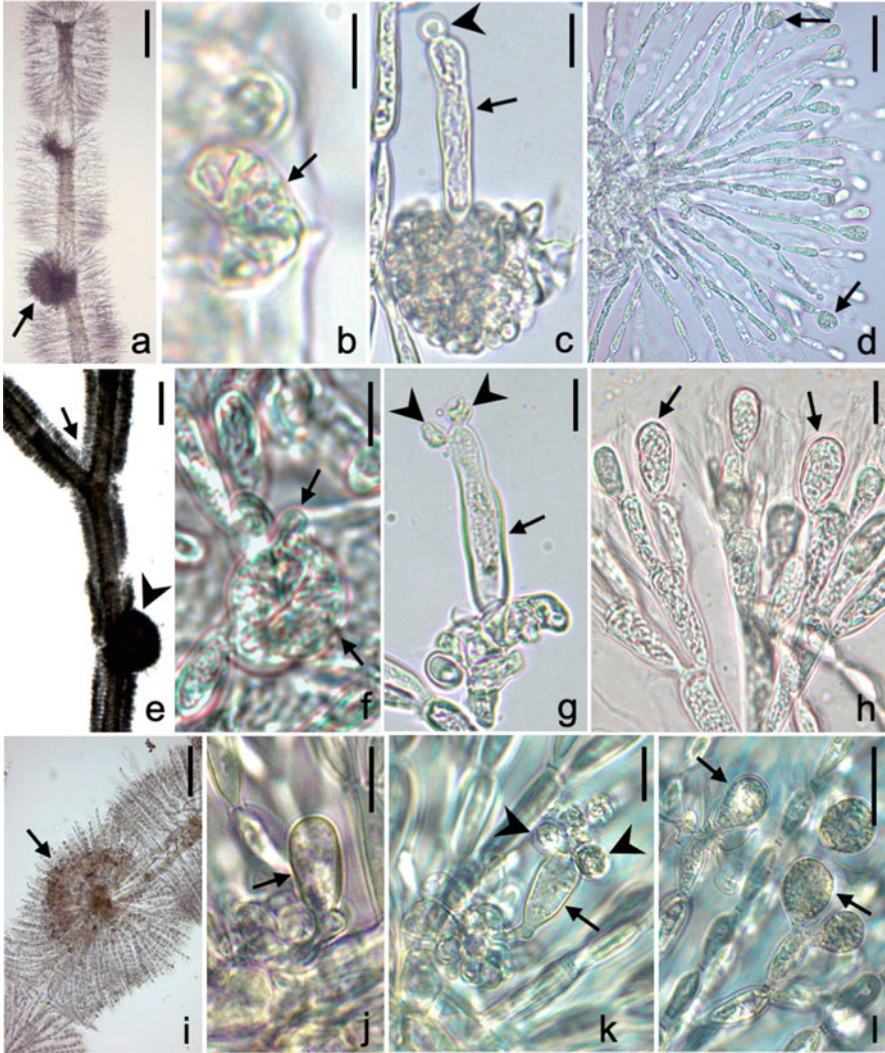
**Synonym:** *Kumanoa tortuosa* (Kumano) ET Johnston, PE Lim, and ML Vis, *Phycologia* 53:336 (2014).

**Type:** PC0452176, FMR Leprieur, no. 1108, date not specified (Lectotype here designated); PC (Isolectotypes).

**Type locality:** French Guiana, near Cayenne, 04.899444° N, 52.330833° W (estimated).

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous or separated, barrel-shaped or obconical, 400–600 µm in diameter; primary fascicles straight, (8–)9–13 cells, proximal cells elongate-ellipsoidal or elongate-cylindrical, distal cells ellipsoidal; secondary fascicles abundant,





**Fig. 5.30** (a–d) *Kumanoa montagnei*: (a) reduced whorls with dense carposporophyte (arrow); (b) young coiled carpogonial branch (arrow); (c) fertilized carpogonium with cylindrical trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa nodiflora*: (e) reduced whorls with pseudodichotomous branching (arrow) and dense carposporophyte (arrowhead); (f) young coiled carpogonial branch (arrows); (g) fertilized carpogonium with ellipsoidal trichogyne (arrow) and attached spermatium (arrowhead); (h) gonimoblast filaments with carposporangia (arrows); (i–l) *Kumanoa novaecaledonensis*: (i) well-developed whorls with loose carposporophyte (arrow); (j) mature carpogonium with clavate trichogyne (arrow); (k) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatia (arrowheads); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (e) = 200 µm; (a, i) = 100 µm; (d) = 25 µm; (l) = 20 µm; (b, c, f, h, j, k) = 10 µm

covering the entire internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 4–6  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–11 disc- or barrel-shaped cells; carpogonium 45–65  $\mu\text{m}$  in length with sessile and cylindrical or clavate trichogynes, 9.0–1.5  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, loose, lower than whorls, 150–230  $\mu\text{m}$  in diameter, 70–100  $\mu\text{m}$  in height; gonimoblast filaments 5–8 cylindrical or ellipsoidal cells; carposporangia obovoidal or ellipsoidal, 10–15  $\mu\text{m}$  in length, 9–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to others with thin fascicle cells (elongate-ellipsoidal or elongate-cylindrical) but differs by the following combination of characters: long carpogonia ( $\geq 45$   $\mu\text{m}$  in length) and loose and small carposporophytes ( $\leq 230$  in diameter and  $\leq 100$  in height) that are lower than whorls and small carposporangia ( $\leq 15$   $\mu\text{m}$  in length,  $\leq 12$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** EU636713 (COI-5P), AY423396 (*rbcL*).

**Distribution:** Asia: Malaysia; South America: French Guiana (Fig. 5.18).

**Key references:** Vis et al. (2004, 2005), Necchi and Vis (2012), Vis et al. (2012), Johnston et al. (2014).

**Remarks:** Sheath et al. (1992) designated specimen PC0738331 as the holotype, but it is not part of Montagne collection at PC presumably because they were unaware of the Montagne collection at the time. One of the syntypes (PC0452176) is here designated as lectotype since it is the one used by Montagne to describe the species. Necchi and Vis (2012) listed *K. tortuosa* as a doubtful species, possible synonym of *K. montagnei*, that is here formally proposed.

***Kumanoa nodiflora*** (Montagne) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.30e–h)

**Basionym:** *Batrachospermum nodiflorum* Montagne, *Ann Sci Nat, Bot*, ser 3, 14: 294 (1850).

**Type:** PC0452169, FMR Leprieur, no. 1107, date not specified (Lectotype here designated); PC (Isolectotypes).

**Type locality:** French Guiana, Cayenne, near Tigres Mountains, 04.914167° N, 52.303056° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls reduced, contiguous, elongate-obconical, 100–300  $\mu\text{m}$  in diameter; primary fascicles straight, 4–7 cells, proximal cells elongate-cylindrical or elongate-ellipsoidal, distal cells ellipsoidal, rarely obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 5–8  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–9 disc- or barrel-shaped cells; carpogonia 30–55  $\mu\text{m}$  in length with sessile and clavate or ellipsoidal trichogynes, 9–13  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, higher than whorls, 200–400  $\mu\text{m}$  in diameter, 90–200  $\mu\text{m}$  in height; gonimoblast filaments with 5–8 cylindrical or ellipsoidal cells; carposporangia obovoidal or ellipsoidal, 15–20  $\mu\text{m}$  in length, 10–13  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to some species with reduced whorls (*K. deminuta*, *K. holtonii*, *K. louisianae*, and *K. mahlacensis*), but differs by the following combination of characters: pseudodichotomous branching, dense carposporophytes that are higher than whorls and relatively long carposporangia ( $\geq 15 \mu\text{m}$  in length).

**Representative sequences in GenBank:** EU636714, EU636715 (COI-5P), AY423398, AY423399 (*rbcL*).

**Distribution:** South America: French Guiana (Fig. 5.18).

**Key references:** Kumano (1990), Vis et al. (2004, 2005), Necchi and Vis (2012), Vis et al. (2012).

**Remarks:** Sheath et al. (1992) designated specimen PC0452168 as the holotype, but it is not part of Montagne collection at PC presumably because they were unaware of the Montagne collection at the time. One of the syntypes (PC0452169) is here designated as lectotype since it is the one used by Montagne to describe the species.

*Kumanoa novaecaledonensis* ML Vis, Necchi, WB Chiasson, and Entwisle, J Phycol 48:754 (2012) (Fig. 5.30i–l)

**Type:** NSW 613968, TJ Entwisle 3211, 6.vii.2003 (Holotype).

**Type locality:** New Caledonia, tributary of River Blanche, at entrance to Riviere Bleue Park, off Noumea-Yate Road, 22.153333° S, 166.734167° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 250–550  $\mu\text{m}$  in diameter; primary fascicles straight, 8–11 cells, proximal cells cylindrical, ellipsoidal or fusiform, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 6–7  $\mu\text{m}$  in diameter; carpogonial branches curved or helically twisted, rarely straight, arising from pericentral cells, composed of 4–9(–13) disc- or barrel-shaped cells; carpogonia 20–40(–48)  $\mu\text{m}$  in length with sessile or stalked, clavate, cylindrical, or ellipsoidal trichogynes, 9–11  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, loose, lower, rarely higher than whorls, (100–)150–250  $\mu\text{m}$  in diameter, 100–150  $\mu\text{m}$  in height; gonimoblast filaments with 3–6 cylindrical or barrel-shaped cells; carposporangia obovoidal, 12–20(–25)  $\mu\text{m}$  in length, 10–13  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from other species by the following combination of characters: irregular branching, well-developed whorls with fascicles  $\geq 8$  cells, secondary fascicles covering the entire internode, curved or helically twisted rarely straight, carpogonial branches, carposporophytes that are dense and typically lower than whorls relatively small ( $\leq 20 \mu\text{m}$  in length,  $\leq 13 \mu\text{m}$  in diameter) carposporangia.

**Representative sequences in GenBank:** JN604912 (COI-5P), FJ386465 (*rbcL*).

**Distribution:** Australasia: Australia; Pacific Islands: New Caledonia (Fig. 5.19).

**Key references:** Entwisle and Foard (1999), Necchi and Vis (2012), Vis et al. (2012).

***Kumanoa procarpa*** (Skuja) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.31a–d)

**Basionym:** *Batrachospermum procarpum* Skuja, *Hedwigia* 71:81 (1931).

**Type:** UPS:BOT:A-724536, O Conde, xi.1928 (Lectotype).

**Type locality:** Brazil, Espírito Santo State, Santa Teresa, 19.936111° S, 40.601389° W.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, contiguous or separated, obconical or barrel-shaped, 150–400 µm in diameter; primary fascicles audouinelloid, curved, 6–10 cells, proximal cells cylindrical, distal cells cylindrical or barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles, 5–8.5 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 6–9 disc- or barrel-shaped cells; carpogonia 35–65 µm in length with sessile and cylindrical or clavate trichogynes, 8–13 µm in diameter; carposporophytes 1–2 per whorl, loose, higher than whorls, 170–330 µm in diameter, 80–170 µm in height; gonimoblast filaments with 4–7 cylindrical cells; carposporangia obovoidal, 10–15 µm in length, 7–10.5 µm in diameter.

**Diagnostic characters:** this species most closely resembles *K. americana* in vegetative morphology (pseudodichotomous branching, well developed whorls, audouinelloid primary fascicles and secondary fascicles covering the entire internode) but differs by having shorter primary fascicles, with  $\leq 10$  cells, longer carpogonia ( $\geq 35$  µm in length), and loose carposporophytes that are higher than whorls.

**Representative sequences in GenBank:** JN604920, (COI-5P), FJ386464 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.19).

**Key references:** Skuja (1931), Necchi and Vis (2012), Vis et al. (2012).

***Kumanoa pseudocarpa*** (Reis) Necchi and ML Vis, *Bibliotheca Phycol* 116:59 (2012) (Fig. 5.31e–h)

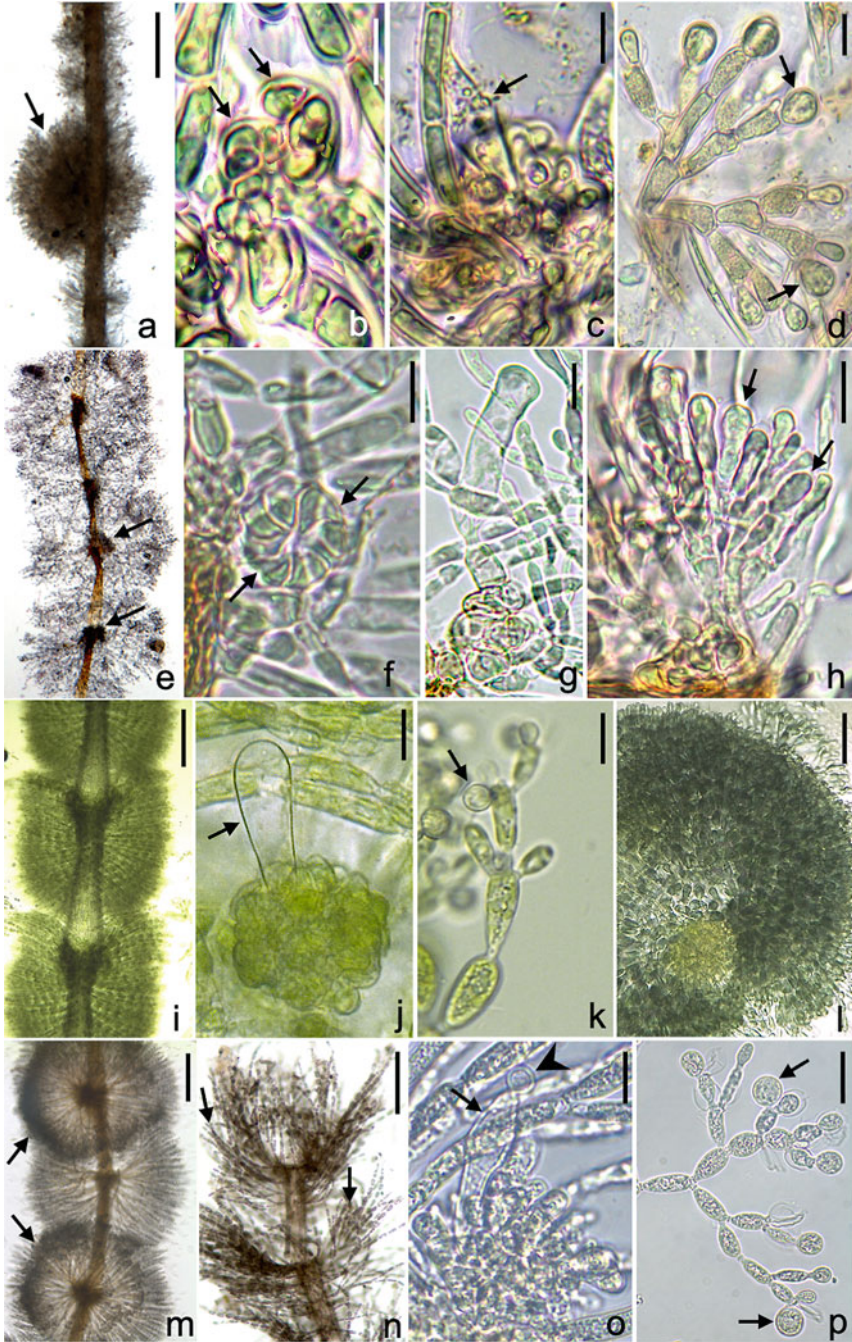
**Basionym:** *Batrachospermum pseudocarpum* Reis, *Bol Soc Brot* 47:146 (1973).

**Type:** COI, MP Reis and MC Alves 604, 07.vii.1970 (Holotype).

**Type locality:** Portugal, Beira Litoral, Ribeira da Louçainha, Espinhal Mountains, near Penela, 40.026111° N, 08.310556° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 400–800 µm in diameter; primary fascicles straight, 8–14 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; monosporangia arranged in fascicles forming spherical or sub-spherical groupings around the nodes on the axes resembling carposporophytes, 100–250 µm in diameter; monosporangia also arising from involucrel filaments, as well as primary and secondary fascicles, ellipsoidal or elongate-obovoidal, 20–25 µm in length, 7–11 µm in diameter; spermatangia rare, spherical or sub-spherical, on primary fascicles, 9–11 µm in diameter; carpogonial branches helically twisted,





**Fig. 5.31** (a–d) *Kumanoa procarpa*: (a) well-developed whorls with loose carposporophyte (arrow); (b) young coiled carpegonial branch (arrows); (c) mature carpegonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa pseudocarpa*: (e) well-developed whorls with spherical

arising from pericentral cells, rarely on rhizoidal filaments, composed of 4–7 disc or barrel-shaped cells; carpogonia 55–70  $\mu\text{m}$  in length with sessile and cylindrical, clavate or bottle-shaped trichogynes, 10.0–12.5  $\mu\text{m}$  in diameter; carposporophytes not observed.

**Diagnostic characters:** this species differs from the others of the genus forming monosporangia (*K. intorta*, *K. lusitanica*, and *K. woitapensis*) in having monosporangial fascicles arising on the nodes of axes and forming spherical or semi-spherical structures resembling carposporophytes, as well as long carpogonia ( $\geq 55$   $\mu\text{m}$  in length) and carposporangia ( $\geq 20$   $\mu\text{m}$  in length).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Portugal (Fig. 5.19).

**Key references:** Reis (1973), Necchi and Vis (2012).

*Kumanoa rwandensis* E Fischer, D Killmann, and D Quandt, Pl Fung Syst 65:153 (2020) (Fig. 5.31i–l)

**Type:** BR, E Fischer 678/17 (AC 068), 8.ix.2017 (Holotype); KOBL (Isotype).

**Type locality:** Rwanda, Southern Province, Nyungwe National Park, Rwasekoko stream in Rwasekoko Swamp, along main road RN6, 2.528778° S, 29.353506° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous or separated, barrel-shaped or obconical, 360–550  $\mu\text{m}$  in diameter. Primary fascicles straight, 8–11 cells, proximal cells cylindrical or ellipsoidal, distal cells elongate-ellipsoidal or fusiform. Secondary fascicles abundant, covering the entire internode; spermatangia spherical, on primary and secondary fascicles, 5–6  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 5–6 cells; carpogonia 32–38(–71)  $\mu\text{m}$  in length with clavate and sessile trichogynes, 10–12  $\mu\text{m}$  in diameter; carposporophytes 1(–2) per whorl, usually higher than whorls, 210–241  $\mu\text{m}$  in diameter, 100–120  $\mu\text{m}$  in height; gonimoblast filaments 6–8 cells; carposporangia obovoidal or ellipsoidal, 6–7  $\mu\text{m}$  in length, 4–4.5 in diameter.

**Diagnostic characters:** this species is most closely related phylogenetically to *K. abiliti*, *K. ambigua*, and *K. gudjewga* (Fig. 5.20) but differs by having thinner distal cells of primary fascicles (length/diameter  $\geq 2.5$ ) that are elongate-



**Fig. 5.31** (continued) or sub-spherical groupings of monosporangia around the nodes (*arrows*); (**f**) young coiled carpogonial branch (*arrows*); (**g**) mature carpogonium with clavate trichogyne (*arrow*); (**h**) grouping of monosporangia on fascicle cells (*arrows*); (**i–l**) *Kumanoa rwandensis*: (**i**) well-developed whorls; (**j**) mature carpogonium with clavate trichogyne; (**k**) distal cells of primary fascicles with terminal spermatangium (*arrow*); (**l**) carposporophyte; (**m–p**) *Kumanoa skujana*: (**m**) well-developed whorls with loose carposporophytes (*arrows*); (**n**) curved primary fascicles (*arrows*); (**o**) fertilized carpogonium with clavate trichogyne (*arrow*) and attached spermatium (*arrowhead*); (**p**) gonimoblast filaments with carposporangia (*arrows*). *Scale bars:* (**a, e, m, n**) = 200  $\mu\text{m}$ ; (**i**) = 100  $\mu\text{m}$ ; (**l**) = 25  $\mu\text{m}$ ; (**h, j, p**) = 20  $\mu\text{m}$ ; (**b–d, f, g, j, k, o**) = 10  $\mu\text{m}$  (Image author: Fig. (**i–l**) E Fischer)



ellipsoidal or fusiform, whereas in those species distal cells are thicker (length/diameter  $\leq 2.5$ ) that are ellipsoidal, obovoidal, or pear-shaped.

**Representative sequences in GenBank:** MT109271, MT109272 (COI-5P), MT109261 (*rbcL*).

**Distribution:** Africa: Rwanda (Fig. 5.19).

**Key reference:** Fischer et al. (2020).

*Kumanoa skujana* (Necchi) Necchi and ML Vis, Phycologia 49:101 (2010) (Fig. 5.31m–p)

**Basionym:** *Batrachospermum skujanum* Necchi, Rev Bras Biol 46:519 (1986).

**Type:** SP, EJ Paula and ML Cristofersen, 13.ii.1975 (Holotype).

**Type locality:** Brazil, São Paulo State, Parelheiros, Evangelista de Souza, 23.934722° S, 46.637500° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or barrel-shaped, 500–1,200  $\mu\text{m}$  in diameter; primary fascicles curved or with distal ends curved, 13–20 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal; secondary fascicles abundant, covering the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, 5.5–7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 8–10 disc- or barrel-shaped cells; carpogonia 30–40  $\mu\text{m}$  in length, with sessile and cylindrical or clavate trichogynes, 7–9  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, loose, higher than whorls, 500–900  $\mu\text{m}$  in diameter, 200–500  $\mu\text{m}$  in height; gonimoblast filaments with 8–12 cylindrical or ellipsoidal cells; carposporangia obovoidal or sub-spherical, 10–15  $\mu\text{m}$  in length, 8.5–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species most closely resembles *K. jolyi* in vegetative morphology (well-developed whorls, non-audouinelloid, and curved primary fascicles with  $\geq 13$  cells) but differs in having loose carposporophytes that are higher than whorls.

**Representative sequences in GenBank:** JN604922 (COI-5P); JN590008 (*rbcL*).

**Distribution:** North America: the USA; South America: Brazil (Fig. 5.19).

**Key references:** Necchi (1986), Necchi and Vis (2012), Vis et al. (2012).

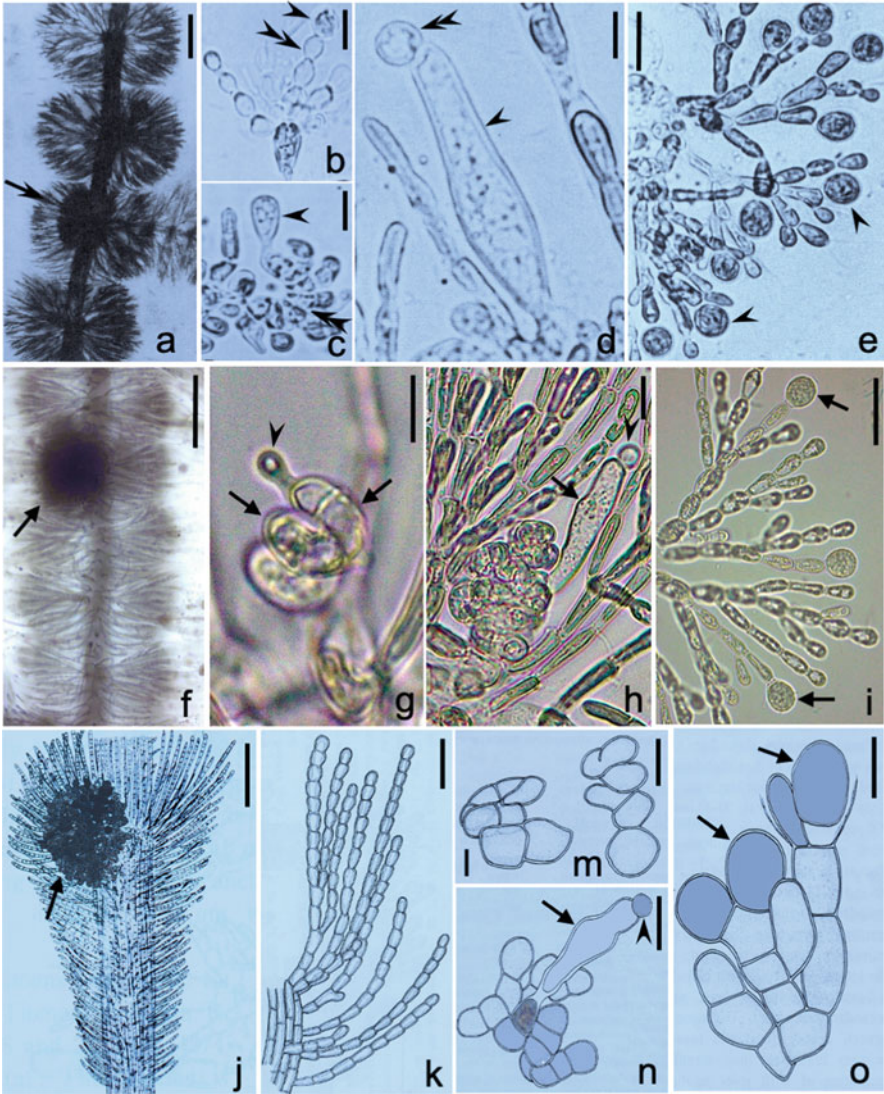
*Kumanoa spermatiophora* (ML Vis and Sheath) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.32a–e)

**Basionym:** *Batrachospermum spermatiophorum* ML Vis and Sheath, Pac Sci 48: 181 (1994).

**Type:** BISH 628882, RG Sheath, 17.viii.1992 (Holotype).

**Type locality:** the USA, Hawaii, Maui Island, Hāna District, tributary to Waiohue Gulch at Pua'aka'a State Wayside and Route 36, 20.816667° N, 156.125278° W.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, barrel-shaped, 550–1200  $\mu\text{m}$  in diameter; primary fascicles straight, 10–16 cells, proximal cells cylindrical or ellipsoidal, distal cells ellipsoidal or obovoidal; secondary fascicles few or abundant, covering half of internode



**Fig. 5.32** (a–e) *Kumanoa spermatiophora*: (a) well-developed whorls with dense carposporophyte (arrowhead); (b) spermatangium (arrowhead) on a colorless spermatiphore (double arrowhead); (c) young coiled carpogonial branch (double arrowhead); (d) fertilized carpogonium with lanceolate trichogyne (arrowhead) and attached spermatium (double arrowhead); (e) gonimoblast filaments with carposporangia (arrowheads); (f–i) *Kumanoa tabagatenensis*: (f) well-developed whorls with loose carposporophyte (arrow); (g) young coiled carpogonial branch (arrows) with developing trichogyne; (h) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (i) gonimoblast filaments with carposporangia (arrows); (j–o) *Kumanoa tiomanensis*: (j) well-developed whorl with dense carposporophyte (arrow); (k) primary fascicle with curved filaments of audouinelloid cells; (l, m) young coiled carpogonial branches; (n) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (o) gonimoblast filaments with carposporangia (arrows). Scale bars: (a) = 250 µm; (f) = 200 µm; (j) = 50 µm; (e, i, l) = 25 µm; (b, c, g, h, k–o) = 10 µm; (d) = 5 µm (Fig. (a–e) reprinted with permission by Wiley from Vis et al. (1994); Fig. (j–o) redrawn from Ratnasabapathy and Kumano (1982a))

length; spermatangia spherical or sub-spherical, on colorless spermatophores, as well as on primary or secondary fascicles, 5–7  $\mu\text{m}$  in diameter; carpogonial branches, curved or less often helically twisted, arising from pericentral cells, composed of (6–)8–12 disc- or barrel-shaped cells; carpogonia 29.5–43  $\mu\text{m}$  in length with stalked or sessile and cylindrical, clavate, or lanceolate trichogynes, 6.5–11.5  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, loose, lower than whorls or rarely reaching the whorl size, 260–450  $\mu\text{m}$  in diameter, 185–300  $\mu\text{m}$  in height; gonimoblast filaments with 4–8 cylindrical or ellipsoidal cells; carposporangia spherical or sub-spherical, 11.5–16  $\mu\text{m}$  in length, 9.5–15.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to other two species (*K. abillii* and *K. virgatodecaisneana*) by having straight or curved, rarely slightly helically twisted carpogonial branches, but differs by specialized spermatangial branches (spermatophores) consisting of colorless distal fascicle cells; it also has longer carpogonial branches (typically).

**Representative sequences in GenBank:** EU636722 (COI-5P); AY424882, KM077034 (*rbcL*).

**Distribution:** Pacific Islands: Hawaii (Fig. 5.19).

**Key references:** Vis et al. (1994), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa tabagatenensis* (Kumano and WA Bowden-Kerby) ML Vis, Necchi, WB Chiasson, and Entwisle, *J Phycol* 48:756 (2012) (Fig. 5.32f–i)

**Basionym:** *Batrachospermum tabagatenense* Kumano and WA Bowden-Kerby, *Jap J Phycol* 34:117 (1986).

**Type:** TNS-AL, WA Bowden-Kerby, 19.v.1984 (Holotype).

**Type locality:** Micronesia, Palau, Babeldaob Island, Nekking, Tabagaten River, 07.523056° N, 134.534444° E.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, contiguous, barrel-shaped, 300–600  $\mu\text{m}$  in diameter; primary fascicles straight, 9–13 cells, proximal cells elongate-ellipsoidal or elongate-cylindrical, distal cells ellipsoidal or cylindrical; secondary fascicles abundant, covering the entire internode; spermatangia sub-spherical or spherical, on primary or secondary fascicles, 4–6  $\mu\text{m}$  in diameter; carpogonial branches, helically twisted, arising from pericentral cells, composed of (6–)8–13 disc- or barrel-shaped cells; carpogonia 50–65  $\mu\text{m}$  in length with sessile and clavate trichogynes, 5–10  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, loose, lower than whorls, 180–300  $\mu\text{m}$  in diameter, 100–200  $\mu\text{m}$  in height; gonimoblast filaments with 5–8 cylindrical or barrel-shaped cells; carposporangia obovoidal or sub-spherical, 12–16  $\mu\text{m}$  in length, 10–14  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from the others in the genus by the following combination of characters: pseudodichotomous branching, well-developed whorls (primary fascicles with  $\geq 9$  cells), helically twisted and long (typically  $\geq 8$  cells) carpogonial branches, carposporophytes that are loose and lower than whorls and small carposporangia ( $\leq 16$   $\mu\text{m}$  in length,  $\leq 14$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** JN604914 (COI-5P); JN590009 (*rbcL*).

**Distribution:** Asia: Philippines; Pacific Islands: Micronesia (Fig. 5.19).

**Key references:** Kumano and Bowden-Kerby (1986), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa tiomanensis* (Kumano and Ratnas) Necchi and ML Vis, *Bibliotheca Phycol* 116:66 (2012) (Fig. 5.32j–o)

**Basionym:** *Batrachospermum tiomanense* Kumano and Ratnas, *Jap J Phycol* 30:18 (1982a).

**Type:** TNS-AL, M Ratnasabapathy, 24.v.1974 (Holotype).

**Type locality:** Malaysia: Pulau Tioman, Sungai Ayer Besar, 02.819167° N, 104.172222° E.

**Description:** thalli monoecious; branching pseudodichotomous; whorls well developed, contiguous, obconical or barrel-shaped, 150–300 µm in diameter; primary fascicles audouinelloid, curved, 11–15 cells, proximal cells cylindrical, distal cells cylindrical or barrel-shaped; secondary fascicles abundant, covering the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles, 4–6 µm in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 6–10 disc- or barrel-shaped cells; carpogonia 37–45 µm in length with sessile and clavate or ellipsoidal trichogynes, 7–10 µm in diameter; carposporophytes 1 per whorl, dense, lower than whorls, 80–150 µm in diameter, 35–80 µm in height; gonimoblast filaments with 3–5 cylindrical cells; carposporangia spherical or sub-spherical, 8–12 µm in length, 6–10 µm in diameter.

**Diagnostic characters:** this species is similar to other species having pseudodichotomous branching and audouinelloid primary fascicles (*K. americana*, *K. cipoensis*, *K. equisetoides*, and *K. procarpa*), but differs by this combination of characters: primary fascicles  $\geq 11$  cells, secondary fascicles covering the entire internode, small ( $\leq 150$  µm in diameter,  $\leq 80$  µm in height) and dense carposporophytes that are lower than whorls and small carposporangia ( $\leq 12$  µm in length,  $\leq 10$  µm in diameter).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia; Pacific Islands: Micronesia (Fig. 5.19).

**Key references:** Ratnasabapathy and Kumano (1982a), Necchi and Vis (2012).

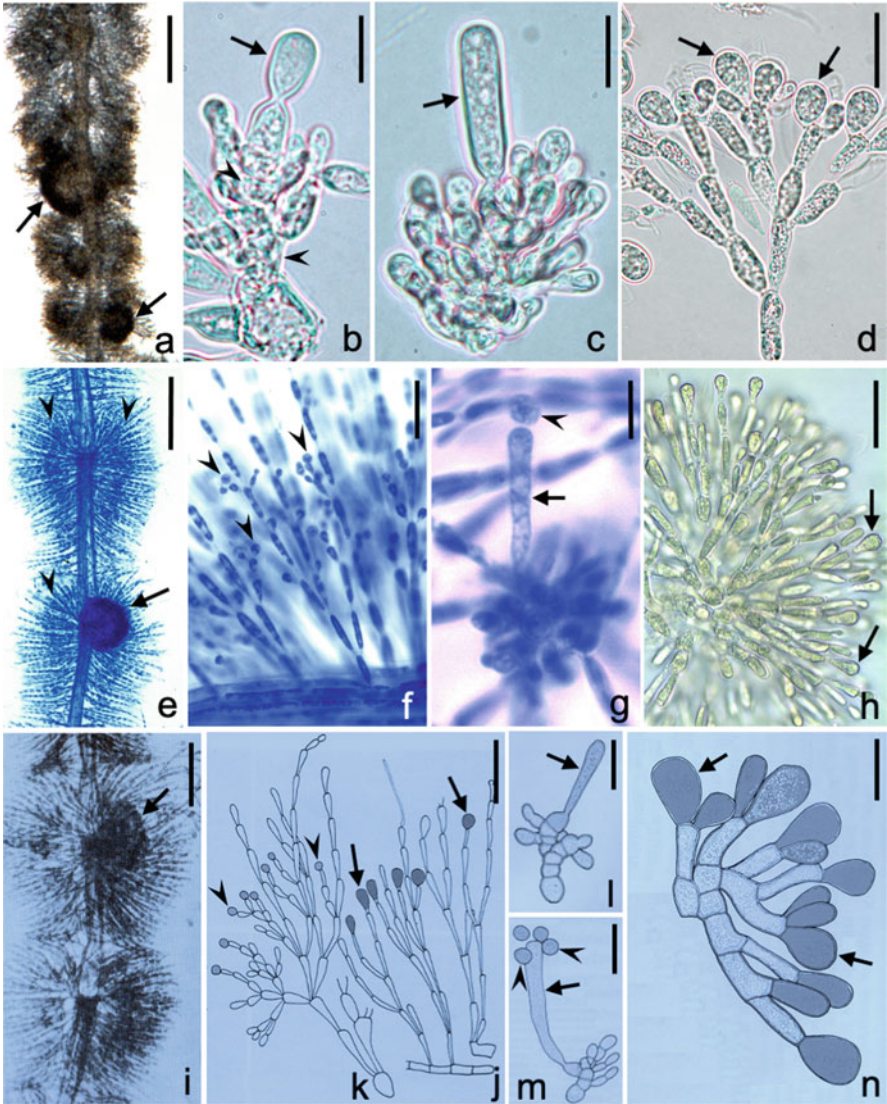
*Kumanoa virgatodecaisneana* (Sirodot) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, *J Phycol* 45:710 (2009) (Fig. 5.33a–d)

**Basionym:** *Batrachospermum virgatodecaisneanum* Sirodot, *Les Batrachospermes*:290 (1884).

**Type:** PC0451819, Thuret collection, S Sirodot, 01.v.1883 (Lectotype here designated); PC (Isolectotypes).

**Type locality:** France, Brittany, near Rennes, mare de la Croix aux Allemands, route de Fougères, 48.350000° N, 01.275000° W (estimated).





**Fig. 5.33** (a–d) *Kumanoa virgatodecaisneana*: (a) well-developed whorls with dense carposporophytes (arrows); (b) young curved carpogonial branch (arrowheads) and developing trichogyne (arrow); (c) mature carpogonium with cylindrical trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Kumanoa vitatta*: (e) well-developed whorls with dense carposporophyte (arrow) and spermatangia in dense arrangement on shorter filaments (arrowheads); (f) spermatangia on filaments shorter than fascicles (arrowheads); (g) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (h) gonimoblast filaments with carposporangia (arrows); (i–n) *Kumanoa woitapensis*: (i) well-developed whorl with loose carposporophyte (arrow); (j, k) primary and secondary fascicles with monosporangia (arrows) and spermatangia (arrowheads); (l) young coiled carpogonial branch with developing trichogyne (arrow); (m) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatia (arrowheads); (n) gonimoblast filaments with carposporangia (arrows). Scale bars: (a) = 250  $\mu\text{m}$ ; (e, i) = 200  $\mu\text{m}$ ; (f) = 50  $\mu\text{m}$ ; (d, h, j, k) = 25  $\mu\text{m}$ ; (l–n) = 20  $\mu\text{m}$ ; (b, c, g) = 10  $\mu\text{m}$  (Fig. (i–n) redrawn from Kumano (1993))

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, barrel-shaped, or sub-spherical, 275–700  $\mu\text{m}$  in diameter; primary fascicles straight, 6–12 cells, proximal cells ellipsoidal or cylindrical, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering two-thirds or the entire internode; spermatangia obovoidal or spherical, on primary or secondary fascicles, 5–7  $\mu\text{m}$  in diameter; carpogonial branches straight, curled or less often helically twisted, arising from pericentral cells, composed of 3–6 disc- or barrel-shaped cells; carpogonia inserted off-center in the carpogonial branch distal cell, 19–35  $\mu\text{m}$  in length with sessile and ellipsoidal, lanceolate, clavate, or cylindrical trichogynes, 5.0–11.5  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, dense, lower than whorls, (80–)120–270(–320)  $\mu\text{m}$  in diameter, (70–)100–230(–285)  $\mu\text{m}$  in height; gonimoblast filaments with 4–7 cylindrical, ellipsoidal, or barrel-shaped cells; carposporangia obovoidal, ellipsoidal, or pear-shaped, 10.5–16.5  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to some species with straight or curved, rarely slightly helically twisted carpogonial branches (*K. abillii*, *K. louisianae*, and *K. spermatiophora*), but differs in having irregular branching, well-developed whorls (primary fascicles with  $\geq 6$  cells), dense carposporophytes that are lower than whorls and small carposporangia ( $\leq 16.5$   $\mu\text{m}$  in length,  $\leq 11$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** AF029148 (*rbcL*).

**Distribution:** Europe: Finland, France, Latvia, Sweden; North America: Canada, the USA; Asia Japan (Fig. 5.19).

**Key references:** Sirodot (1884), Israelson (1942), Eloranta et al. (2011), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa vitatta* (Entwisle and Foard) Entwisle, ML Vis, WB Chiasson, Necchi, and AR Sherwood, J Phycol 45:710 (2009) (Fig. 5.33e–h)

**Basionym:** *Batrachospermum vitattum* Entwisle and Foard, Austral Syst Bot 12: 619 (1999).

**Type:** DNA D0266494, TJ Entwisle 2754, 6.vi.1997 (Holotype); MEL 2045459A (Isotype).

**Type locality:** Australia, Northern Territory, Gubara Pool, tributary of Burdulba Creek, end of Gubara Walk, off Kakadu Highway, between Coinda and Jabiru, Kakadu National Park, 12.795833° S, 132.794444° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical, 350–500  $\mu\text{m}$  in diameter; primary fascicles straight, curved distally, 8–13 cells, proximal cells ellipsoidal or fusiform, distal cells ellipsoidal or obovoidal; secondary fascicles abundant, covering the entire internode; spermatangia forming clusters on short lateral filaments and also on involucrel filaments, 5–6  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells or proximal fascicle cells, composed of 4–7 disc- or barrel-shaped cells; carpogonia 32–40  $\mu\text{m}$  in length and with sessile and clavate or



cylindrical trichogynes, 4–9  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, dense, lower than whorls, 110–260  $\mu\text{m}$  in diameter, 50–150  $\mu\text{m}$  in height; gonimoblast filaments with 4–6 cylindrical or barrel-shaped cells; carposporangia obovoidal or elongate-obovoid, 13–15  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** the most distinguishing character of this species is the presence of specialized spermatangial branches, consisting of short lateral filaments among primary and secondary fascicles bearing spermatangia in clusters. In addition, it differs from other species of *Kumanoa* by this combination of characters: irregular branching, well-developed whorls with fascicles  $\geq 8$  cells, helically twisted and short ( $\leq 7$  cells) carpogonial branches, carposporophytes that are dense and lower than whorls and small carposporangia ( $\leq 15$   $\mu\text{m}$  in length,  $\leq 11$   $\mu\text{m}$  in diameter).

**Representative sequences in GenBank:** JN604911 (COI-5P), JN589010 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.19).

**Key references:** Entwisle and Foard (1999), Necchi and Vis (2012), Vis et al. (2012).

*Kumanoa woitapensis* (Kumano) Necchi and ML Vis, Bibliotheca Phycol 116:71 (2012)

**Basionym:** *Batrachospermum woitapensis* Kumano, Jap J Phycol 31:76 (1983) (Fig. 5.33i–n).

**Type:** TNS-AL, T Yamaguishi 52622, 16.i.1974 (Holotype).

**Type locality:** Papua New Guinea, Central District, Woitape, about 100 km north of Port Moresby, 08.616389° S, 147.242778° E.

**Description:** thalli monoecious; branching irregular; whorls well developed, contiguous, obconical or pear-shaped, 300–700  $\mu\text{m}$  in diameter; primary fascicles straight, 6–12 cells, proximal cells cylindrical or ellipsoidal, distal cells fusiform or ellipsoidal; secondary fascicles abundant, covering the entire internode; monosporangia arising from primary and secondary fascicles, obovoidal or sub-spherical, 10–15  $\mu\text{m}$  in length, 8–10 in diameter; spermatangia spherical or sub-spherical, on primary or secondary fascicles, 5–7  $\mu\text{m}$  in diameter; carpogonial branches helically twisted, arising from pericentral cells, composed of 4–7 disc- or barrel-shaped cells; carpogonia (40–)45–90  $\mu\text{m}$  in length with sessile and clavate trichogynes, 7–10  $\mu\text{m}$  in diameter; carposporophytes 1 per whorl, loose, lower than whorls, 200–500  $\mu\text{m}$  in diameter, 100–250  $\mu\text{m}$  in height; gonimoblast filaments with 4–7 cylindrical cells; carposporangia obovoidal, 14–20  $\mu\text{m}$  in length, 8–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from the others of the genus forming monosporangia (*K. intorta*, *K. lusitanica*, and *K. pseudocarpa*) in having monosporangia exclusively on primary and secondary fascicles, short carpogonial branches ( $\leq 7$  cells), long carpogonia (typically  $\geq 45$   $\mu\text{m}$  in length), and loose carposporophytes that are lower than whorls.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Papua New Guinea (Fig. 5.19).

**Key references:** Kumano (1983), Necchi and Vis (2012).

### *Doubtful Species*

The species listed below could not be confirmed as separate entities in the genus *Kumanoa* to be recognized as distinct from any others here described. Most species were described from India and China, and some were previously treated as doubtful species by Necchi and Vis (2012). The species described from India were formally transferred to *Kumanoa* by Ganesan and West (2013), but with no additional information provided on type specimens, descriptions of diagnostic characters, DNA sequences, or any other allowing to circumscribe them. For all species, type specimens are missing or not available for study and key diagnostic characters were not provided in the protologues.

*Batrachospermum julianum* (Meneghini) Arcangeli, N Giorn Bot Ital 14: 160 (1882).

*Batrachospermum nothocladoideum* SL Xie and ZX Shi, Chin J Ocean Limnol 23: 206 (2005).

*Batrachospermum torridum* Montagne, Ann Sci Nat, Bot, ser 3, 14:292 (1850).

*Batrachospermum torsivum* ZX Shi, Acta Phytotax Sin 32:279 (1994).

*Batrachospermum transitorium* SL Xie and ZX Shi, Chin J Ocean Limnol 23: 207 (2005).

*Kumanoa balakrishnani* (BB Chaugule) EK Ganesan and JA West, Algae 28: 47 (2013).

*Kumanoa dasyphylla* (Skuja ex MS Balakr and BB Chaugule) EK Ganesan and JA West, Algae 28:48 (2013).

*Kumanoa iyengarii* (Skuja ex MS Balakr and BB Chaugule) EK Ganesan and JA West, Algae 28:48 (2013).

*Kumanoa kylinii* (MS Balakr and BB Chaugule) EK Ganesan and JA West, Algae 28:48 (2013).

*Kumanoa mahabaleshwariensis* (MS Balakr and BB Chaugule) EK Ganesan and JA West, Algae 28:48 (2013).

*Kumanoa umamaheswararaoi* (M Baluswami and M Babu) EK Ganesan and JA West, Algae 28:48 (2013).

*Kumanoa zeylanica* (Skuja ex MS Balakr and BB Chaugule) EK Ganesan and JA West, Algae 28:49 (2013).

### *Genera Lemanea and Paralemanea*

*Lemanea* Bory, Ann Muséum d'Hist Nat 12:181 (1808a) nom. cons.

**Type species:** *Lemanea corallina* Bory Ann Muséum d'Hist Nat 12:183 (1808a) nom illeg [= *Lemanea fluviatilis* (L) C Agardh].

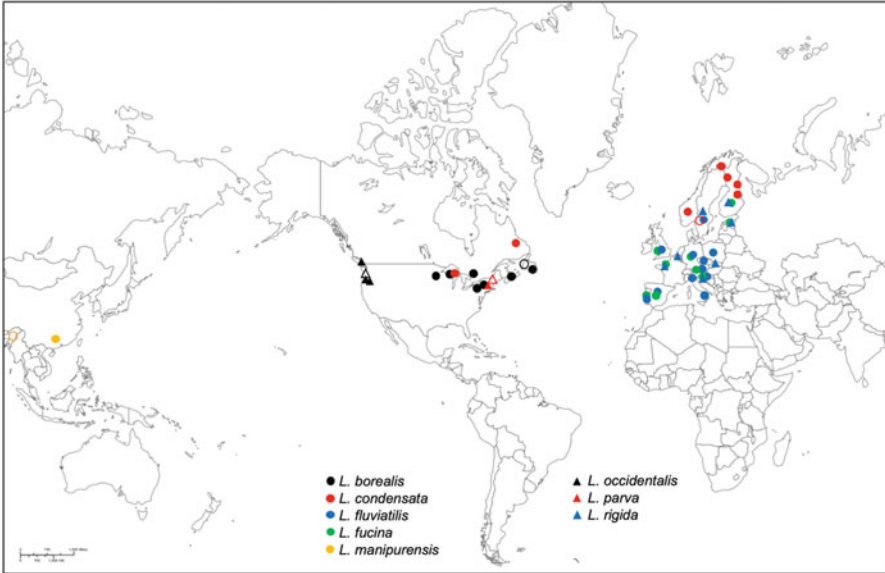
**Description:** thalli monoecious; cartilaginous, pseudoparenchymatous tubular; light green to olive green, violet to black in color; stalked or unstalked, narrow at the base gradually becoming wider, divided into wider nodes and narrower internodes; spermatangia circular papillae variable in number or very rarely fusing into narrow bands around nodes; carpogonia with a thin trichogyne that protrudes through the outer cortex, carposporophytes developing internally in both the internodal and nodal regions; internal construction consisting of central axis without cortical filaments; in longitudinal section, “ray” cells from the central axis to the outer cortex abutting cortex forming either a T- or L-shape; cortex composed of small photosynthetic cells on the outside and one or more layers of larger non-photosynthetic cells on the interior; carposporophytes develop within the thallus in the internodal regions, sometimes extending into the nodal region, often filling this region at maturity; carposporangia obovoidal or ellipsoidal, often produced in chains.

**Diagnostic characters:** this genus can be differentiated from the other tubular genera, *Paralemanea*, *Petrohua*, and *Psilosiphon*, by the combination of spermatangia arranged in circular papillae at the nodes and internal organization with T- or L-shaped ray cells abutting the cortex and a main axis without cortication.

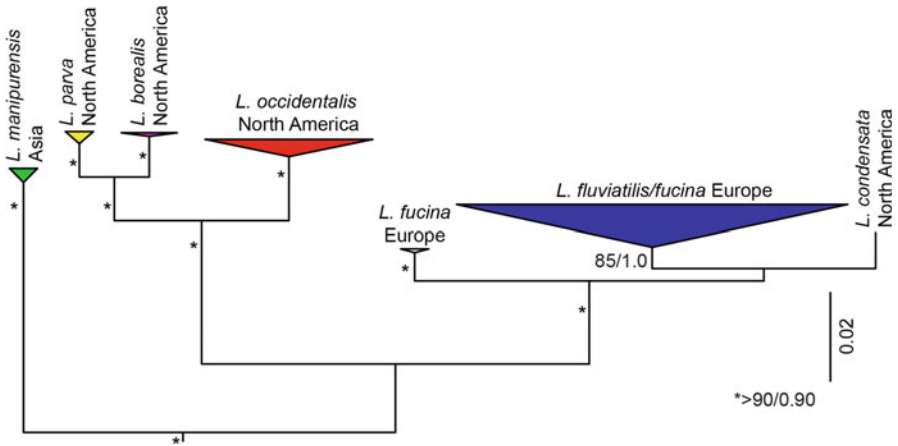
**Habitat:** this genus has a wide ecological distribution in North America and has been reported from streams with the following conditions: pH 4.1–8.2, conductivity 10–300  $\mu\text{S cm}^{-1}$  mean current velocity 38–200  $\text{cm s}^{-1}$  and water temperature 4–17 °C (Vis and Sheath 1992, Sheath and Vis 2015). It is often observed on bedrock or large boulders in dense tufts. In Europe, it has also been collected in streams with varying conditions: pH 6.6–8.8, conductivity 20–980  $\mu\text{S cm}^{-1}$ , mean current velocity 31–311  $\text{cm s}^{-1}$ , and water temperature 6–18 °C (Sheath and Sherwood 2002, Kučera and Marvan 2004, Chiasson et al. 2014, Blagojević et al. 2017).

**Distribution:** Asia, Europe, North America (Fig. 5.34).

**Remarks:** this genus has undergone numerous nomenclatural changes; most notably, species currently in *Paralemanea* were included in the subgenus *Lemanea* and the species currently in *Lemanea* were in the subgenus *Sacheria*. Vis and Sheath (1992) examined the morphology of some type specimens from North America and Europe with a primarily focus on North American specimens. Morphological characters used to distinguish species are not clearly defined for numerous species and rely on thallus color and amount of branching as well as spermatangial papillae number and placement that most likely vary with environmental conditions. Specimens with species names based on morphology have been variously related via DNA sequence data. A comprehensive study of both morphological and DNA sequence data is needed to confidently name some clades in a phylogeny (see below). Comparative morphological data are missing for numerous species and when possible, new morphological data have been added for this synopsis.



**Fig. 5.34** Map showing the distribution of *Lemanea* species. Open symbols represent the type localities



**Fig. 5.35** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Lemanea*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities. Species epithets are based on morphological identifications

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences show six clades and one single specimen branch within the genus (Fig. 5.35). *Lemanea manipurensis* from Asia was an early diverging branch. A clade of three species, *L. occidentalis* sp. nov., *L. parva* stat. nov., and *L. borealis*, from North America was

well supported as well as the individual species clades. A second clade consisting of specimens from Europe with the morphology of *L. fluviatilis* and *L. fucina* as well as a single specimen of *L. condensata* from North America was well supported. Species epithets to be attributed to these clades is uncertain; the clade named *L. condensata* does not have specimens from Europe, the clade named *L. fucina* does not have voucher specimens and the third clade has specimens with morphologies attributed to both *L. fucina* and *L. fluviatilis* and is named with both species until further morphological and molecular are conducted to resolve this conflict. There were numerous *rbcL* sequences for *L. fluviatilis/fucina* clade shown in blue and the intraspecific variation was modest (< 0.93%). Likewise, there were numerous sequence data for *L. occidentalis* sp. nov. with low variation (< 0.62%). There is one species (*L. rigida*) without sequence data that is distinguished by morphology.

Key to the species of the genus *Lemanea*

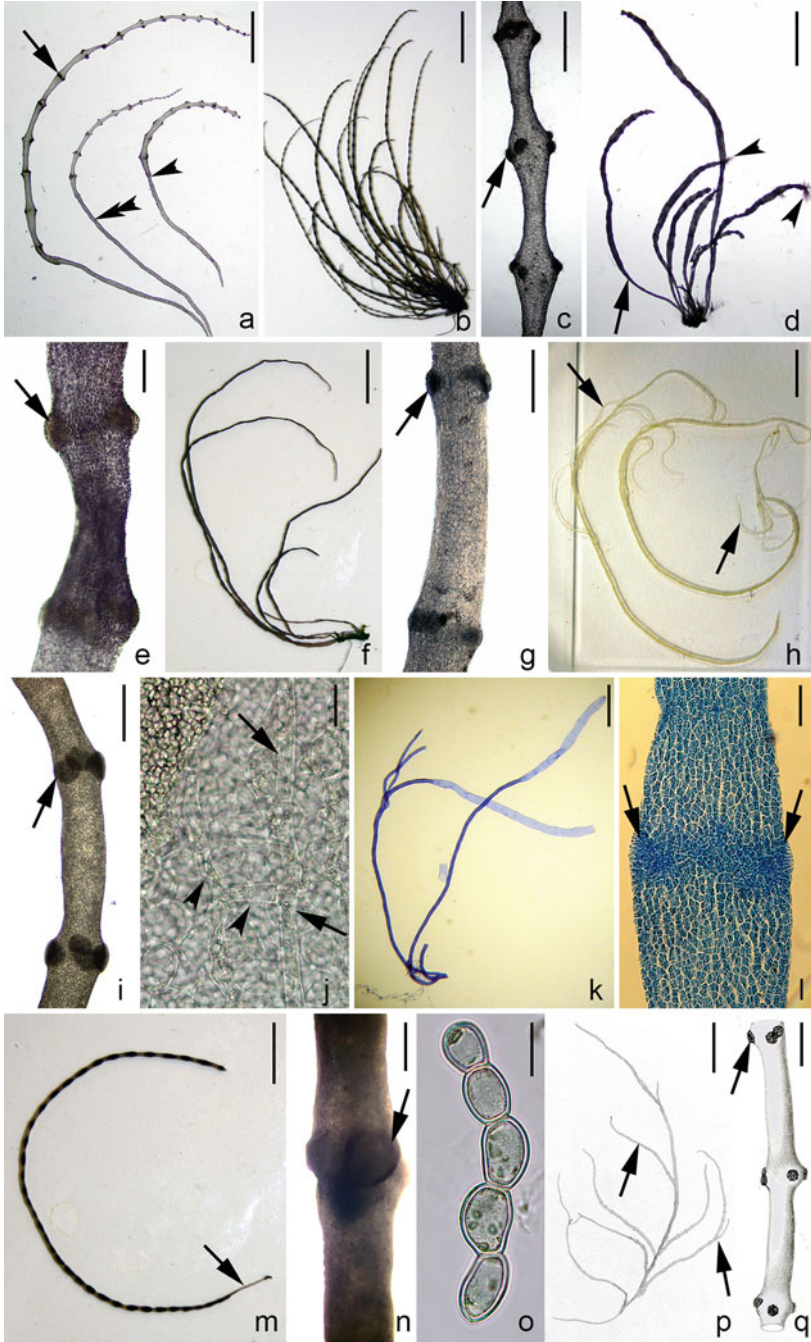
1a	Carposporangia >85 µm in length	<i>L. manipurensis</i>
1b	Carposporangia <85 µm in length or unknown	2
2a	Thalli highly branched (>4 branches per plant) and numerous thalli with branching	3
2b	Thalli unbranched or little branched (only 1 or 2 branches) and few thalli with branching	4
3a	Thalli large (9–15 cm), known distribution in Europe	<i>L. fucina</i>
3b	Thalli small (< 8 cm), known distribution in North America	<i>L. parva</i>
4a	Thalli small at maturity (< 3 cm)	5
4b	Thalli large (>5 cm)	6
5a	Thalli tapering to the base with no evident stalk, known distribution in Europe and North America	<i>L. condensata</i>
5b	Thalli with a slight stalk or only tapering to the base, known distribution in North America	<i>L. borealis</i> (in part)
6a	Thalli stalked or unstalked, known distribution in Europe	7
6b	Thalli stalked, known distribution in North America	8
7a	Thalli stalked, internodal region concave	<i>L. fluviatilis</i>
7b	Thalli unstalked, if branched, branches near base, internodal region cylindrical	<i>L. rigida</i>
8a	Known distribution in western North America	<i>L. occidentalis</i>
8b	Known distribution in eastern North America	<i>L. borealis</i> (in part)

***Lemanea borealis*** Atkinson, Torreyia 4:26 (1904) (Fig. 5.36a–c)

**Type:** NY 00900325, CD Howe, and WF Lang, 09.viii.1901 (Lectotype).

**Type locality:** Canada, Newfoundland and Labrador, Bay of Islands, 49.122° N, 58.128° W (estimated).

**Description:** thalli olive-green, unbranched, unstalked or stalked, nodose, 1–5.5 cm length, 250–665 µm nodal diameter, 150–457 µm internodal diameter; spermatangia arranged in 2–5 circular papillae per node; carpogonia not



**Fig. 5.36** (a–c) *Lemanea borealis*: (a) thalli small with circular spermatangia papillae at nodes (arrow), sometimes with a stalked appearance (arrowhead) or no distinct stalk (double arrowhead); (b) thalli large resembling *L. fluviatilis*; (c) spermatangia in circular papillae at node (arrow) and varying in number; (d, e) *Lemanea condensata*: (d) thalli small with no distinct stalk (arrow) and



described; carpospores ellipsoidal, obovoidal, 25–45 µm in length and 18–25 µm diameter; “Chantransia” cells barrel-shaped 35–45 µm in length, 18–25 µm in diameter.

**Diagnostic characters:** this species has a wide range in size with some populations being small and similar to *L. condensata* and others being larger and similar to *L. fluviatilis*; it can only be distinguished from *L. condensata* based on DNA sequence data and *L. fluviatilis* by geographic range with *L. borealis* in North America and *L. fluviatilis* in Europe.

**Representative sequences in GenBank:** AY575146, AY575147, KM055243 (*rbcL*).

**Distribution:** North America: Canada, the USA (Fig. 5.34).

**Key references:** Atkinson (1904), Vis and Sheath (1992).

**Remarks:** this species is most likely more widespread in North America but only locations with DNA sequence data have been included; likewise, this has been reported from Europe (Eloranta et al. 2011), but these locations were not included in the distribution until DNA sequence data can be used to confirm. Specimens in eastern North America previously referred to *L. fluviatilis* most likely belong to this species.

*Lemanea condensata* Israelson, Symb Bot Upsal 6:20 (1942) (Fig. 5.36d–e)

**Type:** UPS A-000974, G Israelson, 26.vi.1938 (Holotype).

**Type locality:** Sweden, Värmland, Östmark, Vallen, the brook from Amsjön, 59.976132° N, 12.398206° E (estimated).

**Description:** thalli olive-green, brownish, unstalked, unbranched, nodose, 1–2(–3) cm length, 220–350 µm nodal diameter, 100–280 µm internodal diameter; internodes 320–830 µm in length; spermatangial papillae circular, typically 3 per node; carpogonia not described; carposporophytes developing in the internodal region as well as at the nodes; carposporangia not described; “Chantransia” in tufts, branched, cells cylindrical, 18–25 µm in diameter.

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**Fig. 5.36** (continued) having *Audouinella* epiphytic at the tips (*arrowheads*); (**e**) spermatangia in circular papillae at node (*arrow*); (**f, g**) *L. fluviatilis*: (**f**) thalli large with no branching; (**g**) spermatangia in circular papillae at node (*arrow*); (**h–j**) *Lemanea fucina*: (**g**) thalli large with numerous delicate branches per plant (*arrows*); (**i**) spermatangia in circular papillae at node (*arrow*); (**j**) internal structure with the cells of the main axis (*arrows*) without cortication and ray cell in L-shape (*arrowheads*); (**k, l**) *Lemanea manipurensis*: (**i**) plant with sterile region stained dark and fertile region light from alcian blue; (**l**) spermatangial papillae at node fusing to look ring-like (*arrows*); (**m–o**) *Lemanea occidentalis*: (**m**) thalli large and unbranched with distinct stalk (*arrow*); (**n**) spermatangia in circular papillae at node (*arrow*); (**o**) carposporangia obovoidal in a chain; (**p**) *Lemanea parva*: (**p**) thalli small with numerous branches (*arrows*); (**q**) *Lemanea rigida*: (**q**) spermatangia in circular papillae at node (*arrow*) with internodal region not much narrower than node. *Scale bars*: (**a, d, k**) = 2 mm; (**b, f, h, m**) = 1 cm; (**c, g, i**) = 400 µm; (**e**) = 100 µm; (**j, l**) = 50 µm; (**n**) = 200 µm; (**o**) = 20 µm; (**p**) = 5 mm (Image author: Fig. (**b, f, h, m**) W Chiasson; Fig. (**k, l**) J West; Fig. (**p**) reprinted with permission by the publisher (Taylor and Francis) from Vis and Sheath (1992); (**q**) modified from Sirodot (1872))

**Diagnostic characters:** this species is very similar to *L. borealis* and the length from the base to the first node has been used to distinguish these two species in Europe. It can be distinguished from the other species recognized in Europe (*L. fluviatilis*, *L. fucina*, and *L. rigida*) by its small size and for being unstalked and unbranched. Specimens from North America with this morphology have been shown to be distinct from *L. borealis* based on DNA data but the two species cannot be morphologically distinguished.

**Representative sequences in GenBank:** AF029149, MZ043872 (*rbcL*).

**Distribution:** Europe: Finland, Norway, Sweden; North America: Canada and the USA (Fig. 5.34).

**Key references:** Israelson (1942), Eloranta et al. (2011).

**Remarks:** distribution records for *L. borealis*, a morphologically similar species, in northern Europe may also be attributed to this species. Sequence data for two specimens from Newfoundland, Canada, and Michigan, the USA are attributed to this species and distinct from other morphologically similar specimens belonging to *L. borealis* based on DNA sequence data.

*Lemanea fluviatilis* (L) C Agardh, Dispositio algarum Sueciae:25 (1812)  
(Fig. 5.36f, g)

**Basionym:** *Conferva fluviatilis* L Species plantarum Vol. 2:1165 (1753).

**Type:** OXF, tab. 7 fig. 47 from Dillenius's Historia Muscorum

**Type locality:** Europe: "in Europae rivulis fluviisque pacatioribus."

**Description:** thalli olive-green, dark violet to dark brown, stalked, unbranched, nodose, 6–30 cm length, 300–1200(–1600)  $\mu\text{m}$  nodal diameter, internodal diameter slightly narrower becoming swollen and 1700–2000  $\mu\text{m}$  when carposporophytes present; internodes 1–3(–4.5) mm in length; spermatangial papillae circular, typically 3–4 or more per node; carposporangia and "Chantransia" not described.

**Diagnostic characters:** this species is distinguished from other species in Europe based on larger size and being stalked (*L. condensata*), distinct node and internode regions (*L. rigida*), and unbranched (*L. fucina*). However, these characters need to be revisited especially branching which is used to distinguish it from *L. fucina*.

**Representative sequences in GenBank:** AY575156, AY575169, KU343187 (*rbcL*).

**Distribution:** Europe: Austria, Croatia, Czech Republic, France, Germany, Italy, Poland, Spain, Sweden, the UK (Fig. 5.34).

**Key references:** Sheath and Sherwood (2002), Eloranta et al. (2011).

**Remarks:** this species has been reported throughout Europe and there is DNA sequence data from numerous countries; however, specimens with this morphology and those with the *L. fucina* morphology have been shown to be genetically similar such that a revision using both morphological and DNA data is needed. Previous reports of this species from North America should be referred to *L. occidentalis* (western) and *L. borealis* (eastern). Records of this species from

outside Europe need to be confirmed with DNA sequence data and were not included in the distribution of this species.

***Lemanea fucina*** Bory, Ann Muséum d'Hist Nat 12:185 (1808a) (Fig. 5.36h–j)

**Heterotypic synonym:** *Lemanea mamillosa* Kütz., Phycologia germanica:261 (1845).

**Type:** PC0602630, Bory, 1800 (Holotype).

**Type locality:** France, Bretagne, between Vitré and Fourgères, 48.236° N, 1.178° W (estimated).

**Description:** thalli olive-green, highly branched (>6 per plant), stalked, nodose, 9–15 cm length, 465–811 µm nodal diameter, 295–565 µm internodal diameter; internodes 1.4–2.5 mm in length; spermatangial papillae circular, typically 3–5 per node; carpogonia not described; carposporangia in chains, obovoidal, 42–57 µm in length and 32–51 µm diameter; “Chantransia” not described.

**Diagnostic characters:** this species is distinguished from other species in Europe (*L. condensata*, *L. fluviatilis*, and *L. rigida*) based on abundant branching, well-defined nodes and for being stalked. However, the primary character, branching, used to distinguish it from *L. fluviatilis* needs to be revisited.

**Representative sequences in GenBank:** AY575160, KJ825958, KJ825959 (*rbcL*).

**Distribution:** Europe: Croatia, Estonia, Finland, France, Germany, Spain, Sweden, the UK (Fig. 5.34).

**Key references:** Vis and Sheath (1992), Eloranta et al. (2011).

**Remarks:** Herein, *L. mamillosa* has been designated a synonym. Previous researchers have distinguished this species from *L. fucina* based on *L. mamillosa* being very branched and *L. fucina* being branched. However, Bory’s drawing of the type specimen has many branches such that there is no distinction between the two species. The species description is based on measurements provided in Vis and Sheath (1992) for the type specimen and the following specimens: BHO A-0237, A-0239, A-1036, which had the *L. fucina* morphology and similar sequence data. In the distribution data, reports of both *L. fucina* and *L. mamillosa* were recorded.

***Lemanea manipurensis*** Ganesan, JA West, Zuccarello, J Rout, Algae 30:3 (2015) (Fig. 5.36k, l)

**Type:** MEL 2381649, J Rout and M Thajamandhi, 23.xii.2013 (Holotype), MICH1210723, UC2050402 (Isotypes).

**Type locality:** India, Manipur, near Chakpi village in Chakpi River, 24.2666666667° N, 93.8666666667° E.

**Description:** thalli green to dark purple, stalked or unstalked, sparsely branched, nodose, up to 10 cm length, up to 650 µm nodal diameter, no internodal diameter or length reported; spermatangial papillae irregular shaped, sometimes coalescing into rings; carpogonia not described; carposporangia single, terminal on short branched gonimoblast, ellipsoidal, 85–115 µm in length and 38–54 µm diameter; basal “Chantransia” sometimes evident.

**Diagnostic characters:** this species can be distinguished from others by the large carposporangia (>85 µm in length).

**Representative sequences in GenBank:** KP407869, MT297643 (*rbcL*).

**Distribution:** Asia: China, India.

**Key reference:** Ganesan et al. (2015).

**Remarks:** as noted by Ganesan et al. (2015), the morphology of this species is quite similar to four other species (*L. crassa*, *L. ramosa*, *L. simplex*, and *L. sinica*) described from China (see doubtful species below). If future research determines all to represent the same entity, *L. sinica* has priority.

*Lemanea occidentalis* ML Vis and KM Müller sp. nov. (Fig. 5.36m–o)

**Type:** BHO A-0889, E Salomaki, D Lam and M Ashworth, 18.vii.2011 (Holotype); MICH1210867 (Isotype).

**Type locality:** the USA, Oregon, between Jewell and Olney, highway OR 202 under bridge between mile marker 25 and 26, 46.01306° N, 123.67194° W.

**Description:** thalli olive-green, unbranched, stalked, nodose, 2.2–5.5 cm length, 686–845 µm nodal diameter, 448–586 µm internodal diameter; internodes 2.2–2.7 mm in length; spermatangial papillae circular 3–5 per node; carpogonia not observed; carposporangia in chains, obovoidal or ellipsoidal, 25.9–32.9 µm in length and 17.6–24.5 µm diameter; “Chantransia” not observed.

**Diagnostic characters:** this species is very similar in morphology to *L. fluviatilis* from Europe and the revised description of *L. borealis* from eastern North America; geography is useful for distinguishing this species as its distribution in western North America does not overlap other species.

**Etymology:** the species epithet signifies that it occurs in western North America.

**Representative sequences in GenBank:** KC130145 (COI-5P), AF029150, KC134332, MZ043873(*rbcL*).

**Distribution:** North America: western Canada and the USA (Fig. 5.34).

**Remarks:** all specimens from western North America with DNA sequence data belong to this species. Previous researchers have referred specimens from this geographic area to *L. fluviatilis*, but the DNA sequence data distinguishes it as a distinct species.

*Lemanea parva* (ML Vis and Sheath) ML Vis stat. nov. (Fig. 5.36p)

**Basionym:** *Lemanea fucina* var. *parva* ML Vis and Sheath, Phycologia 31: 177 (1992).

**Type:** UBC A8264, RG Sheath and M Koske, 26.v.1989 (Holotype).

**Type locality:** the USA, New Hampshire, 0.2 km north of Rochester, Concheco River crossing Route 16, 43.3221390° N, 70.992724° W (estimated).

**Description:** thalli olive-green, highly branched, stalked, nodose, 2.9–7.1 cm in length, 340–670 µm nodal diameter, spermatangial papillae circular; carpogonia, carposporangia, and “Chantransia” not described.

**Diagnostic characters:** this species differs from all others in North America based on highly branched thalli; it may be distinguished from *L. fucina* as it is smaller

which was originally noted when the variety was described; *L. parva* and *L. fucina* do not geographically overlap and *rbcL* sequence data show them to be genetically distinct.

**Representative sequences in GenBank:** AF029151, MZ043874 (*rbcL*).

**Distribution:** North America: the USA (New Hampshire and Connecticut) (Fig. 5.34).

**Key reference:** Vis and Sheath (1992).

**Remarks:** the variety *L. fucina* var. *parva* is raised to species status based on unique DNA sequence data and potentially the morphological character of highly branched thalli. The morphological characteristics could not be confirmed in the Connecticut specimens as they were small and immature. It is unclear if specimens from North America that are highly branched will be genetically the same such that Oklahoma and Arkansas streams noted in Vis and Sheath (1992) are not listed in the distribution until confirmed by DNA sequence data. This species needs a more detailed analysis of the morphology. The data presented in the tables from Vis and Sheath (1992) combined the measurements for this species and *L. fucina*.

*Lemanea rigida* (Sirodot) De Toni, Sylloge algarum:42 (1897b) (Fig. 5.36q)

**Basionym:** *Sacheria rigida* Sirodot, Ann Sci Nat Sér 5 Bot 16:72 (1872).

**Type:** PC, Sirodot unmounted specimen collection (Syntypes); REN 2078, 2082 (Topotypes).

**Type locality:** France, Brittany, stream in Saint Lazare valley near Montford.

**Description:** thalli red-violet, brownish, olive-green, few branches confined to the base, unstalked, nodose, 5–20 cm length, stout or robust in diameter; spermatangial papillae circular, 3–7 per node, carpogonia, carposporangia, and “Chantransia” not described.

**Diagnostic characters:** this species has been distinguished from other *Lemanea* species in Europe based on stout thalli that are cylindrical with little difference in width between the nodes and internodes.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Belgium, Croatia, Estonia, Finland, France, Slovakia, Sweden (Fig. 5.34).

**Key references:** Sirodot (1872), Eloranta et al. (2011).

**Remarks:** this species has been reported from streams in numerous European countries, but there are few details regarding morphological measurements and qualitative characteristics used to distinguish it from *L. fluviatilis* and *L. fucina*. Vis and Sheath (1992) made a few measurements (stalked, highly branched) of topotype specimens collected by Sirodot that do not agree with the current concept of the species provided in Eloranta et al. (2011) (unstalked, branches confined to base of thallus). New research on morphology and DNA sequence data is needed to determine whether to continue to recognize it as distinct or a synonym of another species.

## ***Doubtful Species***

***Lemanea crassa*** SL Xie and ZX Shi, Acta Bot Sinica 46:884 (2004).

***Lemanea ramosa*** SL Xie and ZX Shi, Acta Bot Sinica 46:884 (2004).

***Lemanea simplex*** CC Jao, Sinensia 12:272 (1941).

***Lemanea sinica*** CC Jao, Sinensia 12:270 (1941).

These four species are only known from the type localities and have numerous characteristics in common with each other and *L. manipurensis* and all five species are from Asia; these species have been differentiated by a combination of plant size, degree of branching and spermatangia in papillae/interrupted rings or contiguous rings, but further molecular and morphological research is required to verify the uniqueness of each; if they are determined to be synonymous, *L. sinica* has nomenclatural priority.

***Lemanea ciliata*** (Sirodot) De Toni, Sylloge algarum:42 (1897b). This species is only known from the type locality and also reported from Poland. Sirodot originally distinguished it from other species primarily based on this species being very hairy. Freshwater red algae may produce hyaline hairs that are hypothesized to be for nutrient uptake (particularly phosphorus) but are not considered taxonomically important. This species is likely a synonymy of one of the other European species which can be confirmed by molecular data.

***Lemanea hispanica*** Budde, Arch Hydrobiol 20:462 (1929). This species has only been reported from the type locality. In the protologue, a brief description and three simple drawings are provided but no distinguishing characteristics from other *Lemanea* species can be assessed. As well, there is no reference to herbarium voucher specimens such that the validity of this species cannot be confirmed.

***Lemanea sudetica*** Kütz, Phycologia germanica: 265 (1845). This species is only known from the type locality and has been reported from the Czech Republic. This species apparently has spermatangial papillae scattered irregularly rather than on the nodes which is its only distinguishing character. It is likely that specimens attributed to the species represent aberrant specimens of one of the other European species, potentially *L. rigida*.

***Paralemanea*** (PC Silva) ML Vis and Sheath, Phycologia 31:177 (1992)

**Basionym:** *Lemanea* subg. *Paralemanea* PC Silva, Taxon 8:62 (1959).

**Type species:** *Lemanea nodosa* Kütz, Species Algarum: 528 (1849)  
[=*Paralemanea catenata* (Kütz) ML Vis and Sheath].

**Description:** thalli monoecious; cartilaginous, pseudoparenchymatous tubular; olive green, violet to black in color; narrow at the base, gradually becoming wider (unstalked) and divided into wider nodes and narrower internodes; spermatangia arranged in rings that is usually a broad, contiguous band around nodes or can be a narrow sometimes interrupted bands; carpogonia not observed in most species, but in the internodes based on the placement of the carposporophytes; mature carposporophytes filling the whole of the internodal



region, sometimes extending into nodal region; internal construction consisting of central axis with abundant cortical filaments; in longitudinal section, “ray” cells from the central axis to the outer cortex simple, not abutting cortex; cortex composed of small photosynthetic cells on the outside and one or more layers of larger non-photosynthetic cells on the interior; carposporophytes develop within the thallus in the internodal regions, often filling this region at maturity; carposporangia sub-spherical, obovoidal, or ellipsoidal, often produced in chains.

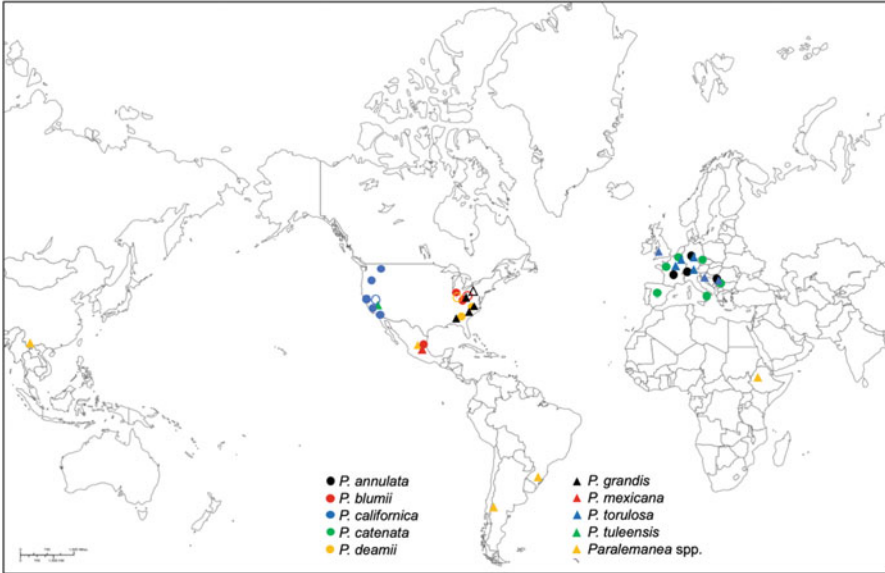
**Diagnostic characters:** this genus can be differentiated from the tubular other genera, *Lemanea*, *Petrohua*, and *Psilosiphon*, by the combination of spermatangia arranged in rings around nodes and internal organization with simple ray cells and cortication around the main axis.

**Habitat:** this genus has a wide ecological distribution in North America and has been reported from streams with the following conditions: pH 5.5–8.6, conductivity 42–500  $\mu\text{S cm}^{-1}$  mean current velocity 18–110  $\text{cm s}^{-1}$  and water temperature 4–17 °C (Sheath and Vis 2015). In Europe, it has also been collected in streams with varying conditions: pH 6.8–9.2, conductivity 70–510  $\mu\text{S cm}^{-1}$ , mean current velocity 105  $\text{cm s}^{-1}$  and water temperature 8–29 °C (Sheath and Sherwood 2002, Kučera and Marvan 2004, Chiasson et al. 2014, Blagojević et al. 2017; Simić and Dordević 2017).

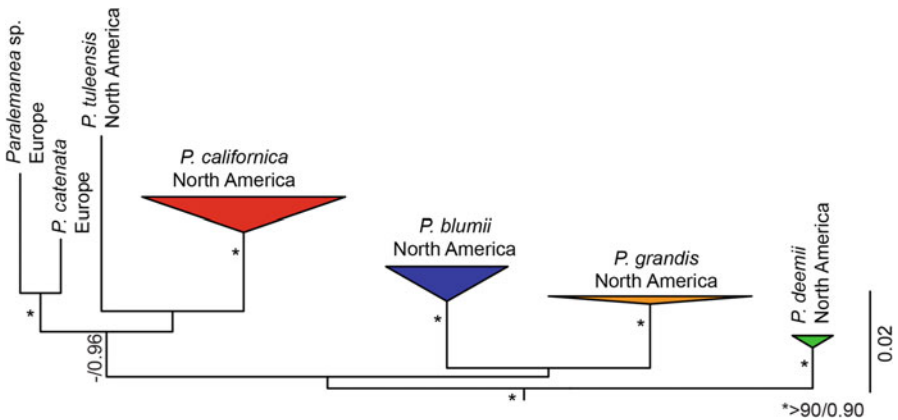
**Distribution:** Africa, Asia, Europe, North America, South America (Fig. 5.37).

**Remarks:** this genus is in need of a comprehensive revision as the most recent (Vis and Sheath 1992) was primarily focused on North America and type specimens from North America and Europe. The morphological characters used to distinguish species are not clearly defined for numerous species and rely on thallus size including the amount of undulation and spermatangial ring characteristics that can vary with thallus age. Comparative morphological data are missing for numerous species, particularly for sexual reproductive structures and carposporophyte, and when possible, new morphological data have been added for this synopsis. For European species, Eloranta et al. (2011) has been followed with three species designated; however, unpublished DNA sequence data suggest the number of species may be greater. Lastly, the genus is easily distinguished based on morphology and is more geographically widespread than the named species and distribution of unnamed species is also noted on the map (Fig. 5.37).

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences show four clades and three single specimen branches within the genus (Fig. 5.38). *Paralemanea catenata* and another unnamed specimen, both from Europe, were well supported as sister and there is substantial *rbcL* genetic variation (3.4%) to suggest they are not the same species. *Paralemanea tuleensis*, *P. californica*, *P. blumii*, *P. grandis*, and *P. deamii* are from North America and their relationships to each other have low support values. For the four species with multiple sequences, the intraspecific *rbcL* genetic variation is moderate ( $\leq 1.1\%$  *rbcL* within *P. blumii* and *P. californica*) to low ( $< 0.4\%$  within *P. deamii* and *P. grandis*). There are three species (*P. annulata*, *P. mexicana*, and *P. torulosa*) without sequence data that are distinguished by morphology.



**Fig. 5.37** Map showing the distribution of *Paralemanea* species. Open symbols represent the type localities. *Paralemanea* spp. shows locations where *Paralemanea* has been reported but the species designation is in doubt; these do not represent the same species but show the wider geographic distribution of the genus



**Fig. 5.38** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Paralemanea* with DNA sequence data. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

Key to the species of the genus *Paralemanea*

1a	Carposporangia >60 µm in diameter	<i>P. deamii</i>
1b	Carposporangia <60 µm in diameter	2
2a	Thalli highly branched, with numerous branches arising from a single point	<i>P. mexicana</i>
2b	Thalli unbranched, or if branched with only a few and not all from the same point	3
3a	Thalli having little differentiation between the diameter of the nodes and internodes, known distribution in Europe	<i>P. torulosa</i>
3b	Thalli having nodes and internodes well distinguished, known distribution in Europe and North America	4
4a	Thalli with spermatangia rings either broad or narrow, forming a contiguous band or interrupted, known distribution in Europe	5
4b	Thalli with spermatangia rings either broad or narrow, forming a contiguous band or interrupted, known distribution in North America	6
5a	Thalli with spermatangia rings broad and forming a contiguous band	<i>P. annulata</i>
5b	Thalli with spermatangia rings narrow and interrupted	<i>P. catenata</i>
6a	Thalli olive-green or black, internode length 1–2 mm	7
6b	Thalli olive-green, internode length >2 mm	8
7a	Thalli black when fresh, known distribution west coast USA	<i>P. tuleensis</i>
7b	Thalli olive-green, known distribution eastern, southeastern USA	<i>P. grandis</i>
8a	Known distribution west coast USA	<i>P. californica</i>
8b	Known distribution midwestern USA, Mexico	<i>P. blumii</i>

*Paralemanea annulata* (Kütz) ML Vis and Sheath, Phycologia 31:177 (1992)  
(Fig. 5.39a)

**Basionym:** *Lemanea annulata* Kütz, Phycologia germanica 261 (1845).

**Type:** L, Herb. Lugd. Bat. 10. Eur. As. #941.149...336, not found.

**Type locality:** Germany, “An Steinen am Wehre in der Saale bei Halle,” On stones at the weir in the Saale near Halle, 51.493386° N, 11.971810° E (estimated).

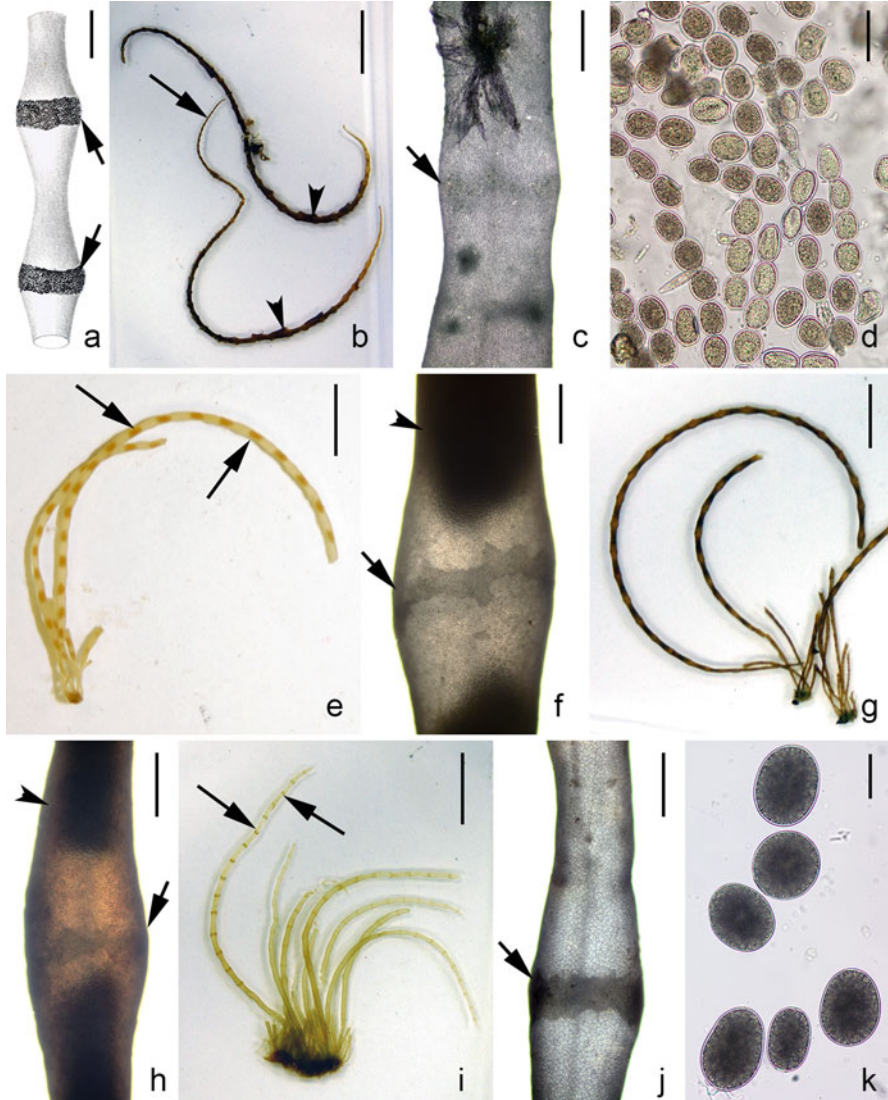
**Description:** thalli violet or dark brown, unbranched, nodose, 8–15 cm in length, < 2 mm nodal diameter, 220–900 µm internodal diameter; spermatangial rings broad, contiguous; carpogonia, carposporangia and “Chantransia” not described.

**Diagnostic characters:** this species has no distinctive characteristics; its geographic distribution overlaps *P. catenata* and *P. torulosa* and may be distinguished from *P. catenata* based on broad versus narrow spermatangial rings and from *P. torulosa* based on nodose versus non-nodose from *P. torulosa*; however, both characters are highly variable and somewhat subjective.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: France, Germany, Serbia, Switzerland (Fig. 5.37).

**Key references:** Vis and Sheath (1992), Eloranta et al. (2011).



**Fig. 5.39** (a) *Paralemanea annulata*: (a) plant nodulose with broad spermatangia rings (arrows); (b–d) *Paralemanea blumii*: (b) thalli with attenuate tips (arrow) and showing macroinvertebrate cases attached (arrowheads); (c) spermatangial ring irregular (arrow); (d) obovoidal carposporangia in chains; (e, f) *Paralemanea californica*: (e) thalli with lighter and darker segments containing carposporophytes (arrows); (f) spermatangial ring irregular (arrow); (g, h) *Paralemanea catenata*: (g) plant habit; (h) plant nodulose with irregular spermatangial ring (arrow); (i–k) *Paralemanea deamii*: (i) plant showing distinct spermatangial rings (arrow); (j) spermatangial ring thick (arrow); (k) large obovoidal carposporangia. Scale bars: (a) = 1 mm; (b, e, g, i) = 1 cm; (c, f, h, j) = 400  $\mu$ m; (d, k) = 50  $\mu$ m (Image author: Fig. (b, e, g) W Chiasson; Fig. (a) modified from Sirodot (1872))

***Paralemanea blumii*** ML Vis sp. nov. (Fig. 5.39b–d)

**Type:** BHO A-0252, N Smucker and J Bonham, 02.vii.2008 (Holotype); MICH1210868 (Isotype); BHO A-1099 (Paratype).

**Type locality:** the USA, Ohio, Shade River Middle branch, 39.21437° N 81.9789° W.

**Description:** thalli olive-green, unbranched, nodose, 5.5–12 cm length, 850–1350 µm nodal diameter, 502–897 µm internodal diameter; internodes 2.4–3.2 mm in length; spermatangial rings narrow and contiguous; carpogonia not described; carposporangia in chains, obovoidal 32–44 µm in length and 27–35 µm diameter; “Chantransia” not observed.

**Diagnostic characters:** this species has no distinctive characteristics; its distribution overlaps *P. deamii* and *P. grandis*; it can be distinguished from *P. deamii* by smaller carposporangia; *P. blumii* has longer plant length and internode length than *P. grandis*, but there were very few specimens measured for each species and their ranges would potentially overlap with more data; therefore, *P. blumii* cannot be reliably distinguished from *P. grandis* without DNA sequence data.

**Etymology:** the species epithet is to honor John L. Blum who conducted in-depth studies of *Paralemanea* in North America.

**Representative sequences in GenBank:** JF701688, MZ043876, MZ043881 (*rbcL*).

**Distribution:** North America: midwestern USA, Mexico (Fig. 5.37).

**Remarks:** specimens were collected from two locations: one was in the early stages of development and the other was mature but covered in epiphytic macroinvertebrate cases. The spermatangial rings were only evident in the younger material (BHO A-1099). DNA sequence data from two culture collections of “Chantransia” stage were similar and attributable to this species (Necchi and Oliveira 2011).

***Paralemanea californica*** Blum, Proc Indiana Acad Sci 103:19 (1997 ‘1994’) (Fig. 5.39e, f)

**Type:** UC2051387 (DC in UC502456), RS Ferris and R Bacigalupi, 29.v.1941 (Holotype).

**Type locality:** California, Mariposa County, four miles north of the Ben Hur Post office, 37.5469° N, 119.9198° W (estimated).

**Description:** thalli olive-green, unbranched, nodose, (2–)3.4–6.5 cm length, (686–)830–1175 µm nodal diameter, (420–)500–850 µm internodal diameter; internodes 2–4 mm in length; spermatangial rings narrow and contiguous; carpogonia not described; carposporangia in chains, obovoidal, 15.4–37 µm in length and 13.2–28.6 µm diameter; “Chantransia” in tufts, branched, cells 11–12 µm in diameter.

**Diagnostic characters:** this species has no distinctive characteristics; its geography overlaps *P. tuleensis* from which it can be distinguished based on plant color when fresh (olive-green versus blackish) and internode length (3.4–6.5 versus 1.0–2.0 mm).

**Representative sequences in GenBank:** MZ043882 (COI-5P); AF029154, AY575144, MZ043878 (*rbcL*).

**Distribution:** North America: western USA (Fig. 5.37).

**Key reference:** Blum (1997 '1994').

**Remarks:** GenBank sequence (MZ043878) is from a toptype collection by N. Ainslie, 27.v.2013, BHO A-1095.

*Paralemanea catenata* (Kütz) ML Vis and Sheath, Phycologia 31:177 (1992)  
(Fig. 5.39g, h)

**Basionym:** *Lemanea catenata* Kütz, Phycologia germanica 261 (1845).

**Type:** L, Herb. Lugd. Bat. 10. Eur. As. #941.149. .. 343; not found.

**Type locality:** Germany, "In Galliae, Germaniae occidentalis fluviis."

**Description:** thalli violet or olive-green, unbranched, nodose, (5–)6.5–30 cm length, 0.7–1.0(–1.5) mm nodal diameter, 540–705 µm internodal diameter; internodes 2.75–4 mm in length; spermatangial rings narrow, sometimes interrupted; carpogonia not described; carposporangia in chains, obovoidal to sub-spherical, 32–36.2 µm in length and 23.7–30 µm diameter; "Chantransia" not described.

**Diagnostic characters:** this species has no distinctive characteristics; its geographic distribution overlaps *P. annulata* and *P. torulosa* and may be distinguished from *P. annulata* based on narrow spermatangial rings versus thick and from *P. torulosa* based on nodose versus non-nodose from *P. torulosa*; however, both characters are highly variable and subjective.

**Representative sequences in GenBank:** KJ825957 (*rbcL*).

**Distribution:** Europe: Belgium, France, Germany, Italy, Serbia, Spain.

**Key references:** Vis and Sheath (1992), Eloranta et al. (2011).

**Remarks:** records of occurrence for this species from China (Xie et al. 2004) and North America (Vis and Sheath 1992 and literature therein) are not included until they can be verified with DNA sequence data. It is likely that these records represent other morphologically similar species.

*Paralemanea deamii* (Blum) ML Vis **comb. nov.** (Fig. 5.39i–k)

**Basionym:** *Lemanea deamii* Blum, Proc Indiana Acad Sci 102:4 (1993).

**Type:** F, JL Blum #4971 18.viii.1989 (Holotype); not found.

**Type locality:** the USA, Indiana, Crawford County, Whiskey Run near Marengo, 38.365489° N, 86.323441° W (estimated).

**Description:** thalli 3.8–13 cm in length, 750–1600 µm nodal diameter; 432–684 µm internodal diameter; internodes 1.7–3 mm in length, spermatangial rings broad in younger thalli, not visible at maturity; carpogonia not described; carposporangia produced in chains but often observed singly, obovoidal to sub-spherical, 79–97 µm in length 60–75 µm diameter; "Chantransia" branched, cells 17–24 µm in diameter.

**Diagnostic characters:** this species is distinguished from all other species by large carposporangia.



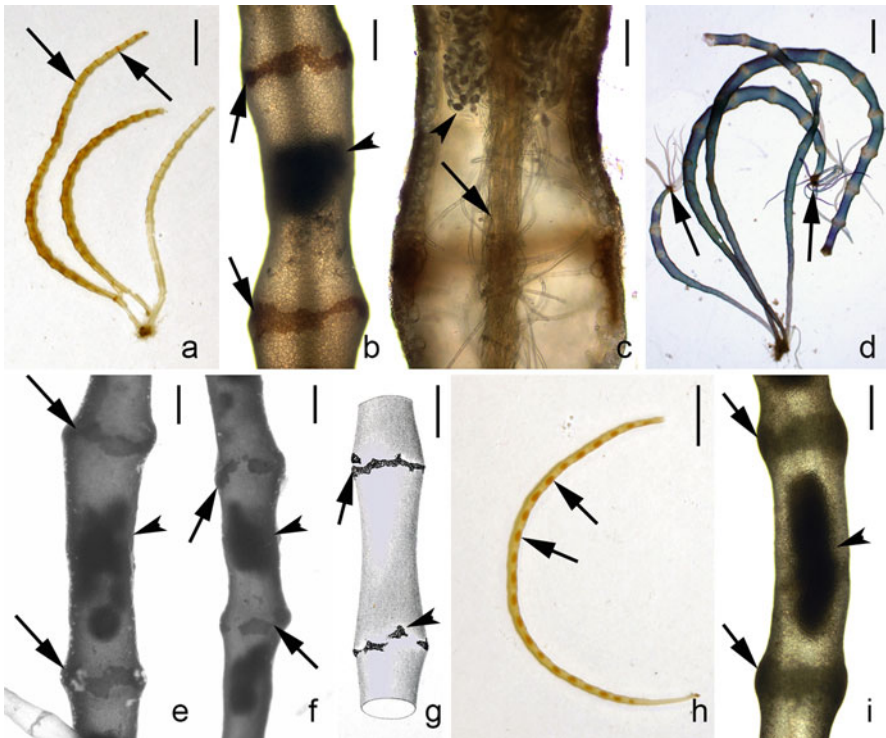
**Representative sequences in GenBank:** KM055335 (COI); DQ523259, GQ285124 (*rbcL*).

**Distribution:** North America: midwestern and eastern USA (Fig. 5.37).

**Key reference:** Blum (1993).

**Remarks:** this species was referenced as *P. deamii* in Kumano (2002), but he did not formally make a new combination and did not provide the necessary information required by ICBN at the time of publication; therefore, a new combination has been designated here.

*Paralemanea grandis* (Wolle) Kumano, Freshwater Red Algae of the World:269 (2002) (Fig. 5.40a–c)



**Fig. 5.40** (a–c) *Paralemanea grandis*: (a) thalli with spermatangia rings at nodes (arrows); (b) irregular, distinct, spermatangial rings (arrows), and internal carposporophyte (arrowhead); (c) internal structure with numerous cortical filaments around the main axis (arrow) and chains of carposporangia in the internodal region (arrowhead); (d–f) *Paralemanea mexicana*: (d) plant with whorls of branches (arrows); (e) irregular spermatangial rings (arrows) and internal carposporophyte (arrowhead); (f) broken spermatangial rings (arrows) and internal carposporophyte (arrowhead); (g) *Paralemanea torulosa*: (g) spermatangia in irregular ring (arrow) and broken ring (arrowhead); (h, i) *Paralemanea tuleensis*: (h) thalli with lighter and darker segments containing carposporophytes (arrows); (i) thick spermatangial rings (arrows) and internal carposporophyte (arrowhead). Scale bars: (a, d, h) = 5 mm; (g) = 1 mm; (b, e, f, i) = 200  $\mu$ m (Image author: Fig. (a, h) W Chiasson; Fig. (g) modified from Sirodot (1872))

**Basionym:** *Entothrix grandis* Wolle, Bull Torrey Bot Club 6:183 (1877).

**Type:** NY 900328, F Wolle, vii.1877 (Lectotype here designated); PH00220326 (Isolectotype).

**Type locality:** the USA, Pennsylvania, Bethlehem, on rocks in the streams, 40.616556° N, 75.365527° W (estimated).

**Description:** thalli olive-green, unbranched, nodose, 3.5–7 cm length, (450–) 586–1159 µm nodal diameter, 442–804 µm internodal diameter; internodes 1.3–1.6 mm in length; spermatangial rings narrow and uninterrupted; carpogonia not described; carposporangia in chains, obovoidal to ellipsoidal 15.4–33(–45) µm in length and 13.2–28.6 µm diameter; “Chantransia” in tufts, branched.

**Diagnostic characters:** this species has no distinctive characteristics; its geographic distribution overlaps *P. deamii* and *P. blumii* and may be distinguished from *P. deamii* based on carpospore size but cannot be reliably distinguished from *P. blumii* without DNA sequence data.

**Representative sequences in GenBank:** DQ449029, DQ523258, MZ043875 (*rbcL*).

**Distribution:** North America: midwestern and southeastern USA (Fig. 5.37).

**Key references:** Atkinson (1890), Vis and Sheath (1992).

**Remarks:** in Vis and Sheath (1992) the specimen at NY was noted to be the holotype; however, this sheet was a set of exsiccatae and as such is now designated the lectotype with all other sheets (Rabenhorst, Algae Europa’s #2538) being isolectotypes.

*Paralemanea mexicana* (Kütz) ML Vis and Sheath, Phycologia 31:177 (1992) (Fig. 5.40d–f)

**Basionym:** *Lemanea mexicana* Kütz Tabulae phycologicae 34 (1857).

**Type:** L4062808, Herb. Lugd. Bat. 10. Eur. As. #941.149 ... 336.

**Type locality:** Mexico, in alpine river, no collector or date, no latitude or longitude estimated.

**Description:** thalli violet, branched with numerous branches from the same point and sometimes re-branched, nodose, (1.5–)3.6–9.0(–11.4) cm in length, (200–) 520–920(–2,280) µm nodal diameter, (184–)360–660(–739) µm internodal diameter; internode length not recorded; spermatangial rings broad and contiguous; carpogonia with pear-shaped trichogynes; carposporangia in chains, obovoidal or ellipsoidal, 18.4–39.2 µm in length and 12.4–24.8 µm diameter; “Chantransia” cells 18–32 µm in diameter.

**Diagnostic characters:** this species can be distinguished from all others based on the whorls of branches.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** North America: Mexico (Fig. 5.37).

**Key references:** Sánchez-Rodríguez and Huerta (1969), Vis and Sheath (1992), Camona and Necchi (2002).

**Remarks:** carposporangia measurements (22–38 × 40–56 µm) from the type collection were not included in the description as they seem to differ from all other material measured and may be incorrect (Camona and Necchi 2002).

*Paralemanea torulosa* (Roth) Sheath and AR Sherwood, The freshwater algal flora of the British Isles 137 (2002) (Fig. 5.40g)

**Basionym:** *Conferva torulosa* Roth, Catalecta botanica 200 (1797b).

**Type:** not found.

**Type locality:** Germany, “Elbingrode in Hercynia” no collector or date.

**Description:** thalli violet or olive-green, unbranched, 5–8(–15) cm in length, not nodose with internodes same diameter as nodes or slightly incised, 500–700(–1000) µm diameter, spermatangial rings narrow and interrupted; carpogonia, carposporangia, and “Chantransia” not described.

**Diagnostic characters:** this species can be distinguished from all others in the genus based on being tubular with little differentiation between nodes and internodes, but this character is somewhat subjective.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Belgium, Croatia, Czech Republic, France, Great Britain, Germany, Serbia.

**Key references:** Sheath and Sherwood (2002), Eloranta et al. (2011).

*Paralemanea tuleensis* Blum, Proc Indiana Acad Sci 103:19 (1997 ‘1994’)  
(as “tulensis”) (Fig. 5.40h, i)

**Type:** UC1599363, JL Blum #4963, 20.ix.1988 (Paratype).

**Type locality:** the USA, California, Tulare County, Springville, North Fork of Tule River at crossing of Highway 190, 36.1396° N, 118.8055° W (estimated).

**Description:** thalli blackish, nodose, 4.2–8.6 cm in length, 560–758 µm nodal diameter, 458–678 µm internodal diameter; internodes 1.0–2.0 mm in length; spermatangial rings broad or narrow, contiguous; carpogonia not described; carposporangia in chains, obovoidal, 15–31 µm in length and 15–24 µm diameter; “Chantransia” cells 13–33 µm in diameter.

**Diagnostic characters:** this species has no distinctive characteristics; its distribution overlaps *P. californica* from which it can be distinguished based on plant color when fresh (blackish versus olive-green) and internode length [1.0–2.0 versus (2.0–)3.4–6.5 mm].

**Representative sequences in GenBank:** MZ043883 (COI-5P); MZ043880 (*rbcL*).

**Distribution:** North America (USA), known from the type locality only (Fig. 5.37).

**Key reference:** Blum (1997 ‘1994’).

**Remarks:** DNA sequence data are from a topotype collection by N. Ainslie, 27.v.2013, BHO A-1097. The holotype (JL Blum #5176, 11.vii.1993) could not be located at UC.

## ***Doubtful Species***

***P. brandegeae*** Blum, Proc Indiana Acad Sci 103:16 (1997 '1994') (as "brandegeei"). In the protologue, the species description is similar to other species; it was distinguished by '...its relatively short internodes and "banded" appearance'; however, the internode length was given as 2–3 mm, which is similar to *P. californica* [2–4 mm in protologue and overlaps (2–)3.4–6.5) for new material] and a banded appearance due to the alternation of nodes with spermatangia and dark areas with carposporophytes is typical of the genus. However, it is not placed in synonym here because more systematic studies of genetic and morphological variation are needed in the genus as a whole.

***P. gardneri*** Blum, Proc Indiana Acad Sci 103:11 (1997 '1994') (as "gardnerii"). In the protologue, this species was distinguished by the spermatangia rings being narrower and interrupted rather than broad and contiguous as in *P. californica*. This character can be variable among specimens within a single collection or season of collection. However, it is not placed in synonym here because more systematic studies of genetic and morphological variation are needed in the genus as a whole.

***P. parishii*** Blum, Proc Indiana Acad Sci 103:17 (1997 '1994'). The description of this species does not provide morphological characters to distinguish it from others; Kumano (2002) in a key utilized the node at which spermatangial rings appear and the number of cortical filaments around the main axis. This information is only available for the species described by Blum and overlaps among species. However, it is not placed in synonym here because more systematic studies of genetic and morphological variation are needed in the genus as a whole.

***P. parvula*** (Sirodot) SL Xie and ZX Shi, Acta Bot Sinica 46: 887 (2004). The original collection of this species was from France by Sirodot and the second authors collected specimens of similar morphology from China. Recent studies of freshwater red algae employing DNA sequence data have revealed that specimens from different continent with similar morphologies are often different species. It is likely with more study that the specimens from China will be determined to represent a distinct species; DNA sequence data could confirm.

## **Genus *Nothocladus***

***Nothocladus*** Skuja, Beih Bot Centralblatt 52:179 (1934)

**Type species (Lectotype):** *Nothocladus nodosus* Skuja Beih Bot Centralblatt 52: 186 (1934).

**Description:** thalli monoecious or dioecious; reddish-brown, olive-drab, sometimes grass-green; consistency mucilaginous or cartilaginous, branching irregular; whorls well developed, sometimes highly reduced; main axis covered by cylindrical cells and infrequently by bulbous cells; primary fascicles with ellipsoidal, cylindrical, or obovoidal, sometimes spherical cells; secondary fascicles few and

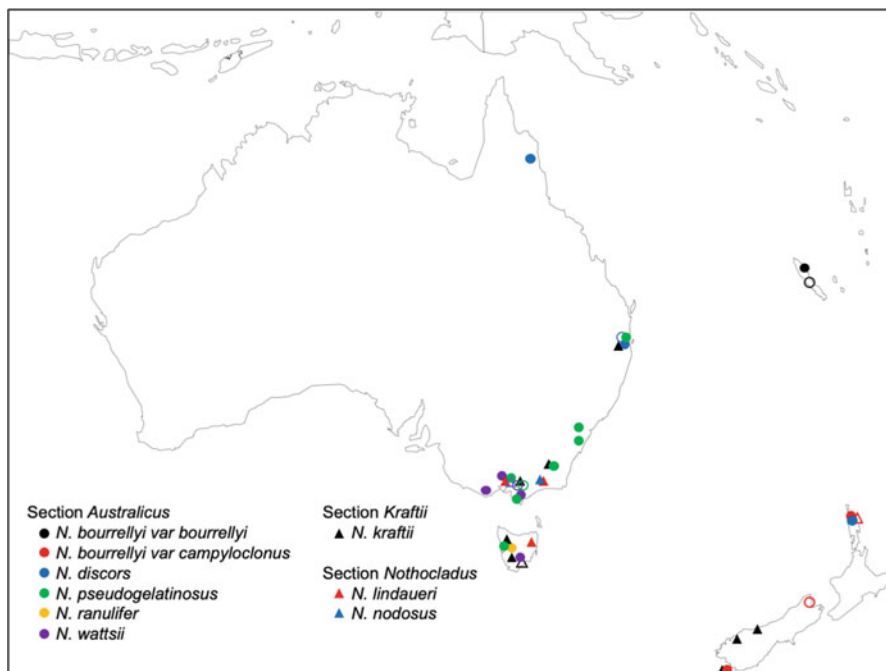
sparse or abundant and covering the entire internode; spermatangia at the tips of primary and secondary fascicles, spherical to sub-spherical; carpogonial branches composed of barrel- or disc-shaped cells or cells of similar shape to the fascicles, few to many celled, straight or sometimes curled, spiralled and twisted, developing from the periaxial cell of primary fascicles; involucrel filaments, short or long; carpogonia with sessile, rarely stalked, clavate, lanceolate, cylindrical, fusiform or ellipsoidal trichogynes; carposporophytes of three types: pedunculate, spherical, small; axial, spherical and hemispherical, large; creeping and diffuse; likewise, gonimoblast filaments densely or loosely arranged with determinate or indeterminate filaments; carposporangia spherical, obovoidal, ellipsoidal, or rarely elongate-obovoidal or clavate, small or large.

**Diagnostic characters:** this genus has a broad morphological description, but it is divided into four sections that are more narrowly circumscribed. *Nothocladus* sections *Australicus* and *Kraftii* are most similar to *Batrachospermum* and *Sheathia* and section *Australicus* can be distinguished based on geographic distribution in Australia (although *Sheathia transpacificica* also occurs in New Zealand); but section *Kraftii* may be distinguished based on carpogonial branches with many short involucrel filaments along its entire length. *Nothocladus* section *Nothocladus* most closely resembles *Tuomeya* with curved or twisted carpogonial branch and cartilaginous consistency but differs in that *Tuomeya* has a compact pseudoparenchymatous construction with small outer cells. Some species of *Nothocladus* section *Theaquus* have highly reduced whorls similar to *Torularia* which cannot be distinguished from this genus and overlap in geographic range. The other species of this section have well-developed whorls, axial carposporophytes, long carpogonia similar to *Virescentia*, but differ in geographic distribution restricted to Australasia.

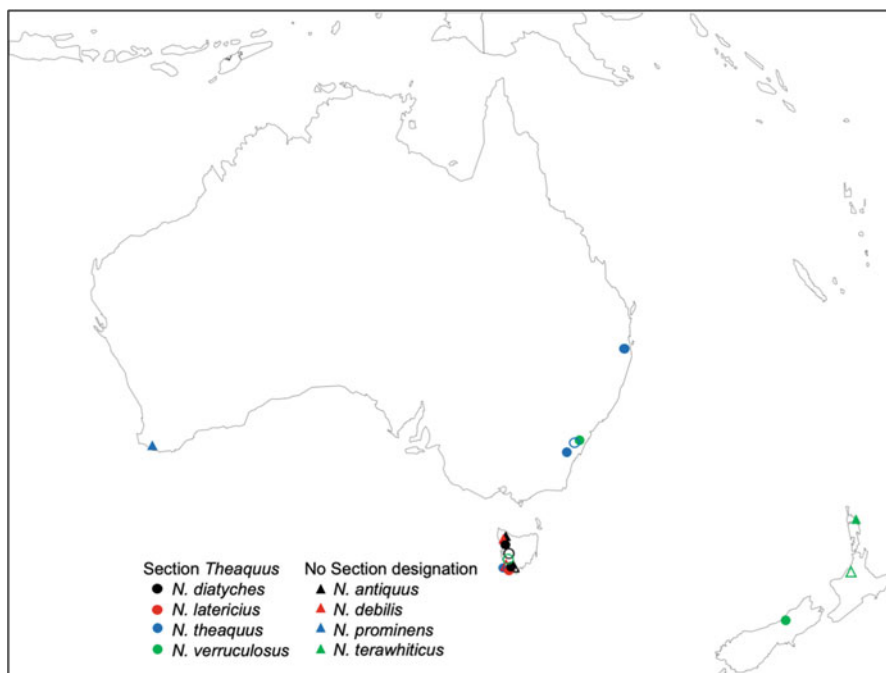
**Habitat:** this genus has been collected in mountain streams, lowland wadable to larger rivers and lakes in Australasia. Many of the species have been recorded from streams and lakes with brown waters. Little detailed data on individual environmental variables have been collected, but when reported, pH has been acidic <6.4, water temperature from 9–18 °C and for *N. wattsii* conductivity was 98–103  $\mu\text{S cm}^{-1}$  (Entwisle 1989a).

**Distribution:** this genus is known exclusively from Australasia except for one species in Africa (*N. afroaustralis*) (Figs. 5.41 and Fig. 5.42).

**Phylogenetic relationships among species:** sequence data of the *rbcL* are available for ten species currently recognized in *Nothocladus* (Fig. 5.43). The genus is paraphyletic if *Torularia* is treated as a genus rather than a section of *Nothocladus*. The four sections are represented in the analysis and section *Kraftii* is most distantly related; it is monospecific, but there is much intraspecific genetic variation (4.4% for *rbcL*). *Nothocladus nodosus*, the only species in section *Nothocladus* with sequence data, is on a long branch. Section *Theaquus* has three species that form a clade, which is only highly supported by posterior probabilities (pp). The multiple sequences for each species (*N. diatyches*, *N. theaquus*, and *N. verruculosus*) are well-supported clades, but on long branches; *N. theaquus* has high intraspecific

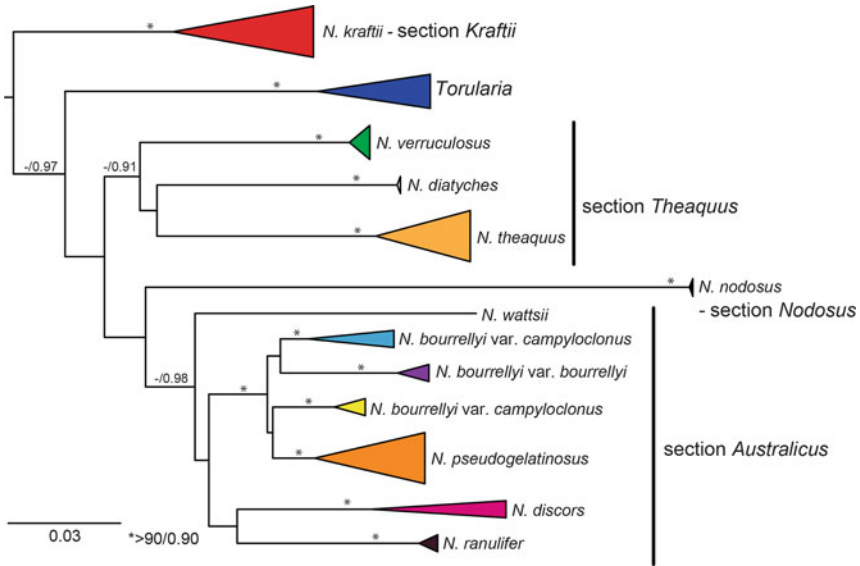


**Fig. 5.41** Map showing the distribution of *Nothocladus* species in sections *Australicus*, *Kraftii* and *Nothocladus*. *Nothocladus afroaustralis* (Section *Nothocladus*) is not shown (Madagascar). Open symbols represent the type localities



**Fig. 5.42** Map showing the distribution of *Nothocladus* species in section *Theaquis* and not assigned to a section. Open symbols represent the type localities





**Fig. 5.43** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Nothocladus* with DNA sequence data. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

genetic variation (3.3%). Likewise, the five species in section *Australicus* form a clade highly supported by pp only. *Nothocladus bourrellyi* has two varieties and they are not monophyletic but the branch with the two varieties has low support; however, there is no support for the placement of *N. bourrellyi* var. *campyloclonus* sister to *N. pseudogelatinosus* (Fig. 5.43). *N. pseudogelatinosus* has much intraspecific variation (4.9%) as does *N. discors* (4.4%). There are two species in section *Nothocladus* and one species in section *Theaquus* distinguished by morphology; four species with unique morphological characteristics have not been assigned to a section. There are 17 species, one with two varieties, in total.

Key to the sections of the genus *Nothocladus*<sup>a</sup>

1a	Whorls highly reduced, primary fascicles tightly adhering to the main axis	Section <i>Theaquus</i> (in part)
1b	Whorls well developed or if reduced primary fascicles not adhering to the main axis	2
2a	Thallus cartilaginous; carpogonial branches twisted or spiralled, carposporophyte diffuse	Section <i>Nothocladus</i>
2b	Thallus mucilaginous or cartilaginous; carpogonial branches straight, carposporophytes compact, or loosely arranged	3
3a	Carposporophytes axial, spherical, or hemispherical, gonimoblast filaments densely arranged	Section <i>Theaquus</i> (in part)

(continued)

3b	Carposporophytes pedunculate, spherical, gonimoblast filaments densely or loosely arranged	4
4a	Carpogonial branches with short involucrel filaments along the entire length	Section <i>Kraftii</i>
4b	Carpogonial branches with involucrel filaments primarily confined to the cells subtending the carpogonium	Section <i>Australasicus</i>

<sup>a</sup>Species keys are provided for each section and those species not assigned to a section

### Section *Australasicus* Entwisle and ML Vis, J Phycol 52:389 (2016)

**Type Species:** *Nothocladus ranulifer* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:391 (2016).

**Description:** thalli monoecious or dioecious, red, brown, green, yellow-green, mucilaginous or cartilaginous, whorls barrel-, disc-, or pear-shaped, contiguous or separate; main axis covered by either cylindrical cells or bulbous cells; spermatangia on primary and sometimes secondary fascicles, spherical to sub-spherical; carpogonial branch arising from the pericentral cell, straight, composed of barrel-shaped cells, carpogonia with clavate, lanceolate, fusiform, or ellipsoidal trichogynes; carposporophytes pedunculate, spherical, compact or rarely loosely arranged with determinate gonimoblast filaments; carposporangia obovoidal, ellipsoidal, sometimes clavate.

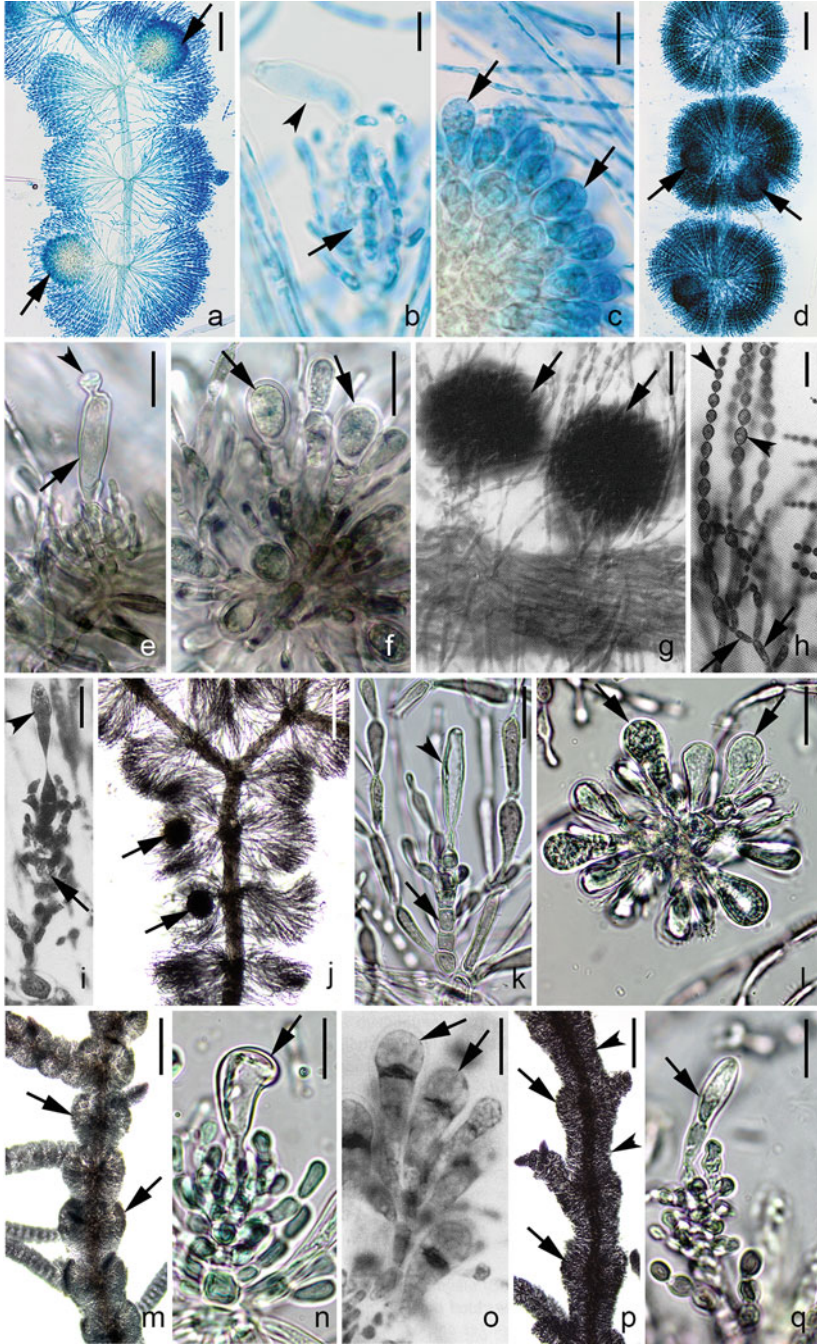
Key to the species of Section *Australasicus*

1a	Main axis covered in bulbous cells	2
1b	Main axis covered in cylindrical cells	3
2a	Fascicles composed of two distinct layers with proximal cells large and ellipsoidal and distal cells small and spherical to obovoidal, 12–20 cells in length	<i>N. discors</i>
2b	Fascicles composed of only of spherical to obovoidal cells, 3–6 cells in length	<i>N. wattsii</i>
3a	Carposporangia >30 µm in length	<i>N. ranulifer</i>
3b	Carposporangia <30 µm in length	4
4a	Carposporophytes often more than 2 per whorl, known from Australia	<i>N. pseudogelatinosus</i>
4b	Carposporophytes 1–2 per whorl, known from New Caledonia and New Zealand	5
5a	Carpogonial branch ≥9 cells, known from New Caledonia	<i>N. bourrellyi</i> var. <i>bourrellyi</i>
4b	Carpogonial branch <9 cells, known from New Zealand	<i>N. bourrellyi</i> var. <i>campyloclonus</i>

***Nothocladus bourrellyi* var. *bourrellyi*** (MP Reis) Entwisle and ML Vis, J Phycol 52:389 (2016) (Fig. 5.44a–c)

**Basionym:** *Batrachospermum bourrellyi* MP Reis in Bourrelly, Rev Hydrobiol Trop 17:51 (1984).

**Type:** Not found.



**Fig. 5.44** (a–c) *Nothocladus bourrellyi* var. *bourrellyi*: (a) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (b) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (c) carposporophyte with obovoidal carposporangia (arrows); (d–f) *Nothocladus bourrellyi* var. *campyloclonus*: (d) spherical whorls with spherical, pedunculate carposporophytes (arrows); (e) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (f) carposporophyte with obovoidal carposporangia (arrows); (g–h) *Nothocladus bourrellyi* var. *campyloclonus*: (g) dark, fuzzy whorls; (h) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (i–l) *Nothocladus bourrellyi* var. *campyloclonus*: (i) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (j) dark, fuzzy whorls; (k) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (l) carposporophyte with obovoidal carposporangia (arrows); (m–q) *Nothocladus bourrellyi* var. *campyloclonus*: (m) dark, fuzzy whorls; (n) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (o) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead); (p) dark, fuzzy whorls; (q) long carpogonial branch (arrow) and carpogonium with clavate bent trichogyne (arrowhead).

**Type locality:** New Caledonia, Province Sud, Rivière Blanche, and Rivière Farino, 21.75° S, 166.18° E (estimated).

**Description:** thalli dioecious; mucilaginous; whorls barrel-shaped, separate, 170–500 µm in diameter; main axis covered by cylindrical cells; primary fascicles 7–12 cells, proximal cells ellipsoidal, distal cells obovoidal; secondary fascicles few to absent; spermatangia 6–8 µm in diameter; carpogonial branches 61–87 µm in length, 9–12 cells; carpogonia 25–45 µm in length with cylindrical or ellipsoidal trichogynes, 7–10 µm in diameter; carposporophytes 1(–2) per whorl, 70–240 µm in diameter; gonimoblast filaments 2–5 cells; carposporangia obovoidal, ellipsoidal, 15–20 µm in length and 10–13 µm diameter.

**Diagnostic characters:** this variety can be distinguished from *N. discors*, *N. watsii*, and *N. ranulifer* based on the combination of main axis cortication cylindrical and shorter carposporangia but is more difficult to differentiate from *N. bourrellyi* var. *campyloclonus* and *N. pseudogelatinosus*; the number of carposporophytes per whorl and carpogonial branch cell number can be used or geographic distribution.

**Representative sequences in GenBank:** FJ386457, KT802843 (*rbcL*).

**Distribution:** Australasia: New Caledonia (Fig. 5.41).

**Key reference:** Entwisle et al. (2016).

*Nothocladus bourrellyi* var. *campyloclonus* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:390 (2016) (Fig. 5.44d–f)

**Basionym:** *Batrachospermum campyloclonum* Entwisle and Foard, Austral Syst Bot 10:364 (1997).

**Type:** MEL 2026362A, F. Wells, vii.1970 (Holotype).

**Type locality:** New Zealand, South Island, Takaka, Waikoropupu Springs, 40.8667° S, 172.7167° E (estimated).

**Description:** thalli monoecious, red, brown, or green; mucilaginous; whorls spherical or barrel-shaped, contiguous, 170–670(–920) µm in diameter; main axis covered by cylindrical cells; primary fascicles 7–16(–25) cells, proximal cells



**Fig. 5.44** (continued) pedunculate carposporophytes (*arrows*); (**e**) fertilized carpogonium with clavate trichogyne (*arrow*) and attached spermatium (*arrowhead*); (**f**) carposporophyte with obovoidal carposporangia (*arrows*); (**g–i**) *Nothocladus discors*: (**g**) spherical, pedunculate carposporophytes (*arrows*); (**h**) primary fascicles with proximal ellipsoidal cells (*arrows*) and spherical distal cells (*arrowheads*); (**i**) long carpogonial branch (*arrow*) and carpogonium with clavate trichogyne (*arrowhead*); (**j–l**) *Nothocladus pseudogelatinosus*: (**j**) barrel-shaped whorls with spherical, pedunculate carposporophytes (*arrows*); (**k**) carpogonial branch (*arrow*) and carpogonium with fusiform trichogyne (*arrowhead*); (**l**) carposporophyte with obovoidal carposporangia (*arrows*); (**m–o**) *Nothocladus ranulifer*: (**m**) barrel-shaped contiguous whorls (*arrows*); (**n**) carpogonium with a curved clavate trichogyne (*arrow*); (**o**) carposporophyte with elongate obovoidal carposporangia (*arrows*); (**p, q**) *Nothocladus watsii*: (**p**) pear-shaped whorls (*arrows*) with abundant secondary fascicles (*arrowheads*); (**q**) carpogonium with elongate ellipsoidal trichogyne (*arrow*). *Scale bars:* (**a, d, g, h, j**) = 100 µm; (**b, c, e, f, i, l, o**) = 20 µm; (**k, n, q**) = 15 µm; (**m, p**) = 300 µm (Fig. (g–i, o) reprinted with permission by CSIRO Publishing from Entwisle and Foard (1997))

ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles few to abundant; spermatangia 4–9  $\mu\text{m}$  in diameter; carpogonial branches 4–11 cells; carpogonia 25–53  $\mu\text{m}$  in length with cylindrical, fusiform or clavate trichogynes, 5–7  $\mu\text{m}$  in diameter; carposporophytes 1–2(–5) per whorl, 60–280(–345)  $\mu\text{m}$  in diameter; gonimoblast filaments 2–6(–12) cells; carposporangia obovoidal or ellipsoidal, 19–32  $\mu\text{m}$  in length and 11–17  $\mu\text{m}$  diameter.

**Diagnostic characters:** this variety can be distinguished from *N. discors*, *N. wattsii*, and *N. ranulifer* based on the combination of main axis cortication cylindrical and shorter carposporangia but is more difficult to differentiate from *N. bourrellyi* var. *bourrellyi* and *N. pseudogelatinosus*; the number of carposporophytes per whorl and carpogonial branch cell number can be used or geographic distribution.

**Representative sequences in GenBank:** KM055324 (COI-5P); KT802844, KT802846, KT802847(*rbcL*).

**Distribution:** Australasia: New Zealand (Fig. 5.41).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus discors* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:391 (2016) (Fig. 5.44g–i)

**Basionym:** *Batrachospermum discors* Entwisle and Foard, Austral Syst Bot 10:341 (1997).

**Type:** MEL 2019946A, TJ Entwisle #2208, 4.x.1993 (Holotype).

**Type locality:** Australia, Queensland, Green Mountains, Lamington National Park, Canungra Creek, 28.2333° S, 153.1333° E.

**Description:** thalli dioecious, yellow-green; mucilaginous; whorls barrel- or disc-shaped, contiguous, 620–1080  $\mu\text{m}$  in diameter; main axis covered by bulbous cells; primary fascicles 12–22 cells, proximal cells ellipsoidal, distal cells obovoidal to spherical; secondary fascicles abundant; spermatangia on primary and secondary fascicles 7–9  $\mu\text{m}$  in diameter; carpogonial branches 5–14 cells; carpogonia (30–)44–60  $\mu\text{m}$  in length with cylindrical, fusiform, or clavate trichogynes, 8–14  $\mu\text{m}$  in diameter; carposporophytes, 1–2 per whorl, 120–185  $\mu\text{m}$  in diameter; gonimoblast filaments 4–5 cells; carposporangia obovoidal, 17–22  $\mu\text{m}$  in length and 8–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species can be distinguished based primarily on fascicles composed of two distinct cell layers with proximal cells ellipsoidal and distal cells obovoidal to spherical and secondarily on the main axis covered by bulbous cells.

**Representative sequences in GenBank:** KT802759 (COI-5P); AF257778, KT802850 (*rbcL*).

**Distribution:** Australasia: Australia, New Zealand (Fig. 5.41).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus pseudogelatinosus* (Entwisle and ML Vis) Entwisle and ML Vis, J Phycol 52:590 (2016) (Fig. 5.44j–l)



**Basionym:** *Batrachospermum pseudogelatinosum* Entwisle and ML Vis, J Phycol 37:1181 (2000).

**Type:** MEL2046213A, T Entwisle #2894, 3.ii.1998 (Holotype).

**Type locality:** Australia, Victoria, Warburton, Dammans Road, Yarra River, 37.75° S, 145.70° E (estimated).

**Description:** thalli monoecious (rarely dioecious), olive-green, rarely red or brown; whorls barrel- or disc-shaped, contiguous, (305–)400–1000(–1100) µm in diameter; main axis covered by cylindrical cells; primary fascicles 8–17(–22) cells, proximal cells ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia on primary fascicles 5–6 µm in diameter; carpogonial branches 41.6–68.1 µm in length, 10–14 cells; carpogonia 35–67 µm in length with cylindrical, fusiform, or clavate trichogynes, 4–6 µm in diameter; carposporophytes, 1–5 per whorl, 80–190 µm in diameter; gonimoblast filaments 2–4 cells; carposporangia obovoidal, 12–28 µm in length and 7–15 µm in diameter.

**Diagnostic characters:** this species can be distinguished from *N. discors*, *N. watsii*, and *N. ranulifer* based on the combination of main axis cortication cylindrical and shorter carposporangia but overlaps the two varieties of *N. bourrellyi* in most characters; number of carposporophytes per whorl or geographic distribution can be used for identification.

**Representative sequences in GenBank:** KM055329, KT802761 (COI-5P); AF209982, AF209983, AY297052 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.41).

**Key references:** Entwisle (1989a), Entwisle and Foard (1997), Vis and Entwisle (2000), Entwisle et al. (2016).

**Remarks:** older references such as Entwisle (1989a) and Entwisle and Foard (1997) referred to this species as *Batrachospermum gelatinosum* until DNA sequence data became available. *Batrachospermum gelatinosum* is only present in the northern hemisphere based on DNA sequence data.

*Nothocladus ranulifer* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:391 (2016) (Fig. 5.44m–o)

**Basionym:** *Batrachospermum ranuliferum* Entwisle and Foard, Austral Syst Bot 10: 347 (1997).

**Type:** NSW A008809, F Perrin, ii.1928, (Holotype).

**Type locality:** Australia, Tasmania, tributary of Adam and Gordon Rivers, Eve River, 42.700° S, 146.300° E.

**Description:** thalli monoecious, olive-green; whorls, spherical, barrel-, or disc-shaped, contiguous, 270–330 µm in diameter; main axis covered by cylindrical cells; primary fascicles 7–9 cells, proximal cells ellipsoidal, distal cells obovoidal; secondary fascicles abundant; spermatangia on primary fascicles 3–5 µm in diameter; carpogonial branches 4–5 cells; carpogonia 25–46 µm in length with curved, ellipsoidal, or clavate trichogynes, 8–10 µm in diameter;



carposporophytes, 1–4 per whorl, 130–160  $\mu\text{m}$  in diameter; carposporangia clavate or elongate-obovoidal 36–46  $\mu\text{m}$  in length and 12–18  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinguished based on the much longer length of the carposporangia than the other species of the section.

**Representative sequences in GenBank:** KP330467, KT802860 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.41).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus watsii* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:390 (2016) (Fig. 5.44p, q)

**Basionym:** *Batrachospermum watsii* Entwisle and Foard, Austral Syst Bot 10: 374 (1997).

**Type:** MEL2026652, TJ Entwisle #961, 24.xi.1986 (Holotype).

**Type locality:** Australia, Victoria, Maroondah Reservoir catchment, Road 1, Slip Creek, 37.6833° S, 145.5833° E.

**Description:** thalli dioecious, dark brown; cartilaginous; whorls, barrel- to pear-shaped, contiguous, 150–450  $\mu\text{m}$  in diameter; main axis covered by bulbous cells; primary fascicles 3–6 spherical to obovoidal cells; secondary fascicles abundant; spermatangia on primary and secondary fascicles 5–6  $\mu\text{m}$  in diameter; carpogonial branches 3–7 cells; carpogonia 20–56  $\mu\text{m}$  in length with clavate to elongate-ellipsoidal trichogynes, 5–8  $\mu\text{m}$  in diameter; carposporophytes diffuse; carposporangia obovoidal or ellipsoidal, 8–15  $\mu\text{m}$  in length and 5–8  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species and *N. discors* are distinguished from other species based on bulbous cortication of the main axis; it differs from *N. discors* in having only spherical to obovoidal fascicle cells.

**Representative sequences in GenBank:** KT802765 (COI-5P); KT802866 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.41).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

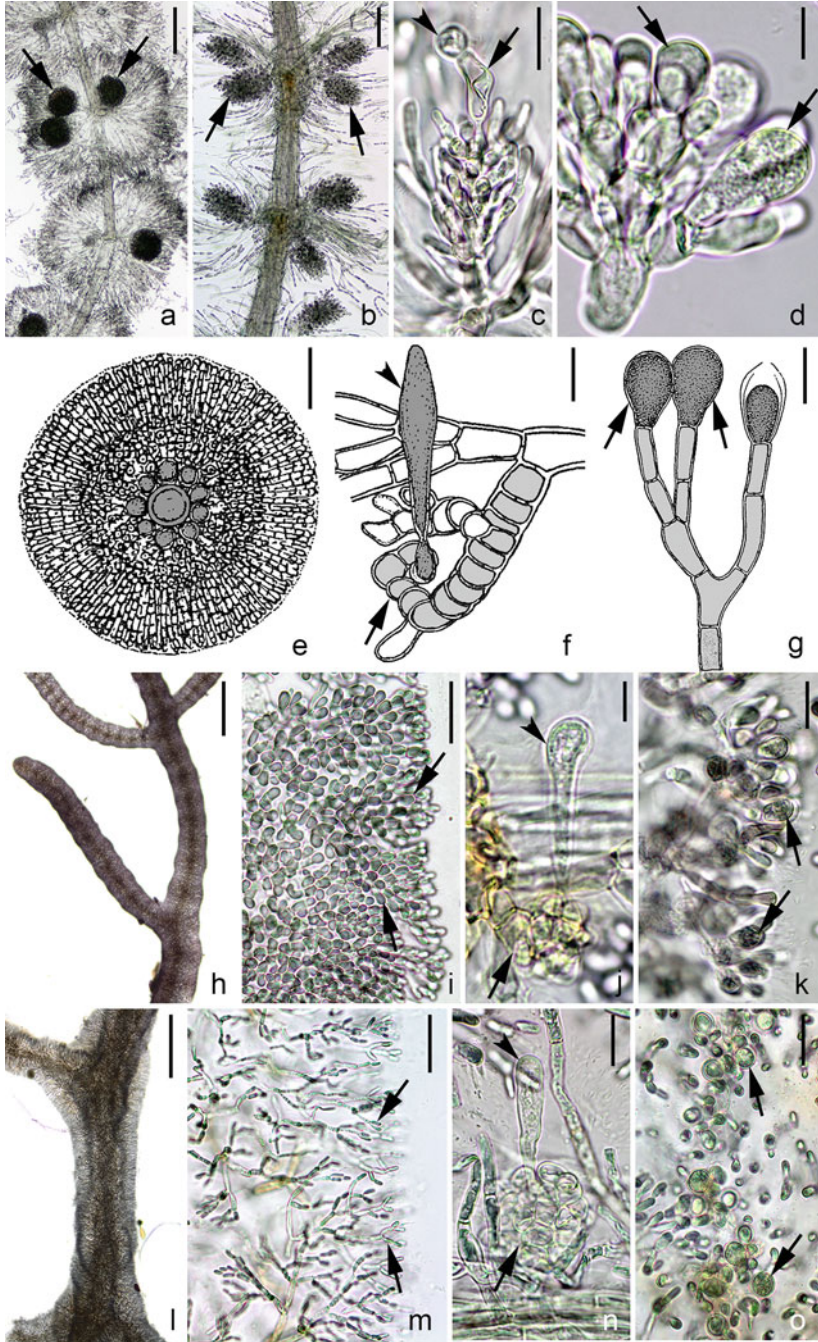
**Remarks:** further investigation of the unique diffuse carposporophyte with few small carposporangia is warranted especially since related species all have compact pedunculate carposporophytes with abundant carposporangia.

**Section *Kraftii*** Entwisle and ML Vis, J Phycol 52:391 (2016)

**Type species:** *Nothocladus kraftii* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:391 (2016).

**Description:** same as the species.

*Nothocladus kraftii* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:391 (2016) (Fig. 5.45a–d)



**Fig. 5.45** (a–d) *Nothocladus kraftii*: (a) spherical whorls with multiple spherical, pedunculate carposporophytes (arrows); (b) conspicuous carposporogonial branches (arrows) with clusters of involucral filaments along the entire branch; (c) fertilized carposporogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) carposporophyte with obovoidal carposporangia

**Basionym:** *Batrachospermum kraftii* Entwisle and Foard, Austral Syst Bot 10: 344 (1997).

**Type:** MEL 2027351, GT Kraft, 27.xii.1992 (Holotype).

**Type locality:** Australia, Tasmania, Hartz Mountain area, Arve River, 43.2167° S, 146.7667° E.

**Description:** thalli dioecious, olive-green or brown; mucilaginous, whorls barrel- to disc-shaped, contiguous, 420–1300 µm in diameter; main axis covered by cylindrical cells; primary fascicles 11–20 cells, proximal cells cylindrical, ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles few; spermatangia 5–8 µm in diameter; carpogonial branches 56.3–64.2 µm in length, 5–14 cells; carpogonia 20–40 µm in length with straight or bent ellipsoidal trichogynes, 6–11 µm in diameter; carposporophytes spherical, 1–2(–3) per whorl, 85–260 µm in diameter; gonimoblast filaments 2–4 cells; carposporangia obovoidal 18–26 µm in length and 7–14 µm in diameter.

**Diagnostic characters:** this species can be distinguished based on carpogonial branches with short involucrel filaments along the entire length of the branch.

**Representative sequences in GenBank:** KT802760 (COI-5P); FJ386461, KT802851, KT802854 (*rbcL*).

**Distribution:** Australasia: Australia, New Zealand (Fig. 5.41).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

**Remarks:** this species shows much genetic variation and is divided into two clades differing in geography (New Zealand and Australia), but morphological characters overlap.

### *Nothocladus* section *Nothocladus*

**Basionym:** *Nothocladus* Skuja, Beih Bot Centralbl 52:186 (1934).

**Type species:** *Nothocladus nodosus* Skuja Beih Bot Centralbl 52:186 (1934).

**Description:** thalli monoecious, cartilaginous, whorls dense, compressed, and indistinct; main axis covered by cylindrical cells; spermatangia on primary and sometimes secondary fascicles, spherical to sub-spherical; carpogonial branches arising from the pericentral cell, curved, twisted, or curled; carpogonia with ellipsoidal, clavate, or lanceolate trichogynes; carposporophytes with

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**Fig. 5.45** (continued) (*arrows*); (**e–g**) *Nothocladus afroaustralis*: (**e**) cross section showing a dense arrangement of fascicle cells; (**f**) long-celled curled carpogonial branch (*arrow*) and carpogonium with lanceolate trichogyne (*arrowhead*); (**g**) gonimoblast filaments with obovoidal carposporangia (*arrow*); (**h–k**) *Nothocladus lindaueri*: (**h**) compressed and indistinct whorls; (**i**) densely arranged fascicles with obovoidal to spherical cells (*arrows*); (**j**) twisted carpogonial branch (*arrow*) and carpogonium with clavate trichogyne (*arrowhead*); (**k**) carposporangia (*arrowheads*) along indeterminate gonimoblast filaments at thallus surface; (**l–o**) *Nothocladus nodosus*: (**l**) compressed and indistinct whorls; (**m**) fascicle cells with ellipsoidal to obovoidal cells (*arrows*) embedded in a gelatinous matrix; (**n**) carpogonial branch twisted into a knot (*arrow*) and carpogonium with clavate trichogyne (*arrowhead*); (**o**) carposporangia (*arrowheads*) along indeterminate gonimoblast filaments at thallus surface. *Scale bars*: (**a**) = 200 µm; (**b**) = 100 µm; (**c**, **k**, **n**, **o**) = 20 µm; (**d**, **f**, **g**, **j**) = 10 µm; (**e**, **m**) = 50 µm; (**h**, **l**) = 400 µm; (**i**) = 40 µm (Fig. (e–g) modified from Skuja (1964))

indeterminate gonimoblast filaments; carposporangia obovoidal, pear-shaped, or ellipsoidal.

Key to the species of section *Nothocladus*

1a	Thalli small, distal fascicle cells sub-spherical to obovoidal	<i>N. lindaueri</i>
1b	Thalli large, distal fascicle cells ellipsoidal	2
2a	Carpogonial branch <9 cells, known from Australia	<i>N. nodosus</i>
2b	Carpogonial branch $\geq 12$ cells, known from Africa	<i>N. afroaustralis</i>

*Nothocladus afroaustralis* Skuja, Rev Algol 7: 310 (1964) (Fig. 5.45e–g)

**Type:** Decary, 12.vii.1932 (Holotype) not found in PC or UPS.

**Type locality:** Madagascar, Tôlanaro (formerly Fort-Dauphin), in river Mamery, 25.033° S, 46.983° E (estimated).

**Description:** thalli monoecious; whorls 200–350(–450)  $\mu\text{m}$  in diameter; primary fascicles 8–9 cells, proximal cells ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia 3.5–4.5  $\mu\text{m}$  in diameter; carpogonial branches  $\geq 12$  cells; carpogonia 30–40(–60)  $\mu\text{m}$  in length with clavate to lanceolate trichogynes, 5.5–8  $\mu\text{m}$  in diameter; carposporophyte with indeterminate gonimoblast filaments 4–7 cells; carposporangia obovoidal or pear-shaped 15–27.5  $\mu\text{m}$  in length and 12–15  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinguished from the other two species based on the length of the carpogonial branch and geographic distribution; in addition, it differs from *N. lindaueri* in the shape of the fascicle cells.

**Representative sequences in GenBank:** no sequence data available.

**Distribution:** Africa: Madagascar, known from the type locality only (not shown on map).

**Key references:** Skuja (1964), Entwisle et al. (2016).

**Remarks:** this species is only known from the type locality and protologue of Skuja (1964); it is in need of more research to compare with other species of *Nothocladus* and *Tuomeya*. The cross sectional drawing indicates that it is more pseudoparenchymatous like *Tuomeya* and unlike *N. lindaueri* and *N. nodosus* in which the fascicle tips are not fused. DNA sequence data could provide biogeographic insights since *Nothocladus* is only known from Australasia and this one location in Africa.

*Nothocladus lindaueri* Skuja, Acta Horti Bot Univ Latv 14:11 (1944) (Fig. 5.45h–k)

**Type:** UPS A-003737, VW Lindauer, 01.xii.1937 (Lectotype); NSW288112 (Isotype).

**Type locality:** New Zealand, North Island, Waitagi Falls, 35.277955° S, 174.051724° E (estimated).

**Description:** thalli monoecious, reddish-brown to olive-green; whorls 100–600  $\mu\text{m}$  in diameter; primary fascicles obovoidal, sub-spherical 4–7(–9) cells; secondary fascicles abundant; spermatangia 3–4  $\mu\text{m}$  in diameter; carpogonial branches 4–9

cells; carpogonia 20–40  $\mu\text{m}$  in length with lanceolate trichogynes, 17–18  $\mu\text{m}$  in diameter; carposporophyte with indeterminate gonimoblast filaments 6–8 cells; carposporangia obovoidal 8–14  $\mu\text{m}$  in length and 6–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from *N. nodosus* based on smaller, more densely branched thalli and fascicle cells that are obovoidal to sub-spherical, especially the tip cells; it may be distinguished from *N. afroaustralis* based on shorter carpogonial branches and geographic distribution.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia, New Zealand (Fig. 5.41).

**Key references:** Skuja (1944), Entwisle et al. (2016).

*Nothocladus nodosus* Skuja, Beih Bot Centralbl 52:186 (1934) (Fig. 5.45l–o)

**Type:** UPS A-003750, H Watts, 1884 (Lectotype).

**Type locality:** Australia, Victoria, Melbourne, Collingwood, Yarra River, 37.806237° S, 145.001892° E (estimated).

**Description:** thalli monoecious, reddish-brown to olive-green; whorls 250–1000  $\mu\text{m}$  in diameter; primary fascicles ellipsoidal 7–12 cells; secondary fascicles abundant; spermatangia 5.5–7  $\mu\text{m}$  in diameter; carpogonial branches 4–9 cells; carpogonia 35–55  $\mu\text{m}$  in length with ellipsoidal to clavate trichogynes, 9–12  $\mu\text{m}$  in diameter; carposporophyte with indeterminate gonimoblast filaments 3–8 cells; carposporangia obovoidal or ellipsoidal 10–15  $\mu\text{m}$  in length and 7–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species differs from *N. lindaueri* based on larger, more open branched thalli and fascicle cells that are cylindrical to ellipsoidal, especially the tip cells; it may be distinguished from *N. afroaustralis* based on shorter carpogonial branches and geographic distribution.

**Representative sequences in GenBank:** KM055334 (COI-5P); AF029152, KT802855 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.41).

**Key references:** Skuja (1934), Entwisle et al. (2016).

*Nothocladus* section *Theaquus* Entwisle and ML Vis, J Phycol 52:392 (2016)

**Type species:** *Nothocladus theaquus* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:392 (2016).

**Description:** species with reduced or well-developed whorls; primary fascicles short or long; secondary fascicles rare to abundant; spermatangia spherical, sub-spherical on primary and sometime secondary fascicles; carpogonial branches short; carpogonia with fusiform, ellipsoidal, clavate trichogynes; carposporophytes large, axial, spherical to hemispherical; gonimoblast filaments densely or loosely arranged, composed of 2–4(–5) barrel-shaped to cylindrical cells; carposporangia spherical to obovoidal.



Key to the species of section *Theaquus*

1a	Whorls reduced; primary fascicles composed of $\leq 6$ cells	2
1b	Whorls well developed; primary fascicles composed of $>7$ cells	3
2a	Primary fascicles composed of 4–6 cells	<i>N. diatyches</i>
2b	Primary fascicles composed of 2 cells, rarely 4	<i>N. latericius</i>
3a	Carposporophytes compact, spherical	<i>N. theaquus</i>
3b	Carposporophytes loosely arranged, semispherical	<i>N. verruculosus</i>

*Nothocladus diatyches* (Entwisle) Entwisle and ML Vis, J Phycol 52:392 (2016) (Fig. 5.46a–c)

**Basionym:** *Batrachospermum diatyches* Entwisle, Muelleria 7: 426 (1992).

**Type:** MEL 1587821A, PA Tyler, 10.iii.1998 (holotype).

**Type locality:** Australia, north-central Tasmania, Lake Meston, 41.900831° S, 146.228010° E (estimated).

**Description:** thalli monoecious, dark brown; whorls reduced, 70–110  $\mu\text{m}$  in diameter; primary fascicles unbranched, 4–6 cylindrical cells; secondary fascicles rare; spermatangia 6–8  $\mu\text{m}$  in diameter; carpogonial branches 2–3 cells; carpogonia 44–46  $\mu\text{m}$  in length with fusiform to obovoidal trichogynes, 5–10  $\mu\text{m}$  in diameter; carposporophytes spherical, 1 per whorl, 80–220  $\mu\text{m}$  in diameter; carposporangia obovoidal, spherical 15–19  $\mu\text{m}$  in length and  $\sim 18$   $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species can be distinguished from *N. theaquus* and *N. verruculosus* based on reduced rather than well-developed whorls; it differs from *N. latericius* in having longer-celled fascicles and the thallus apical cell overtopped by fascicles.

**Representative sequences in GenBank:** KT802758 (COI-5P); KT802848, KT802849 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle (1992), Entwisle et al. (2016).

*Nothocladus latericius* (Entwisle) Entwisle and ML Vis, J Phycol 52:392 (2016) (Fig. 5.46d–g)

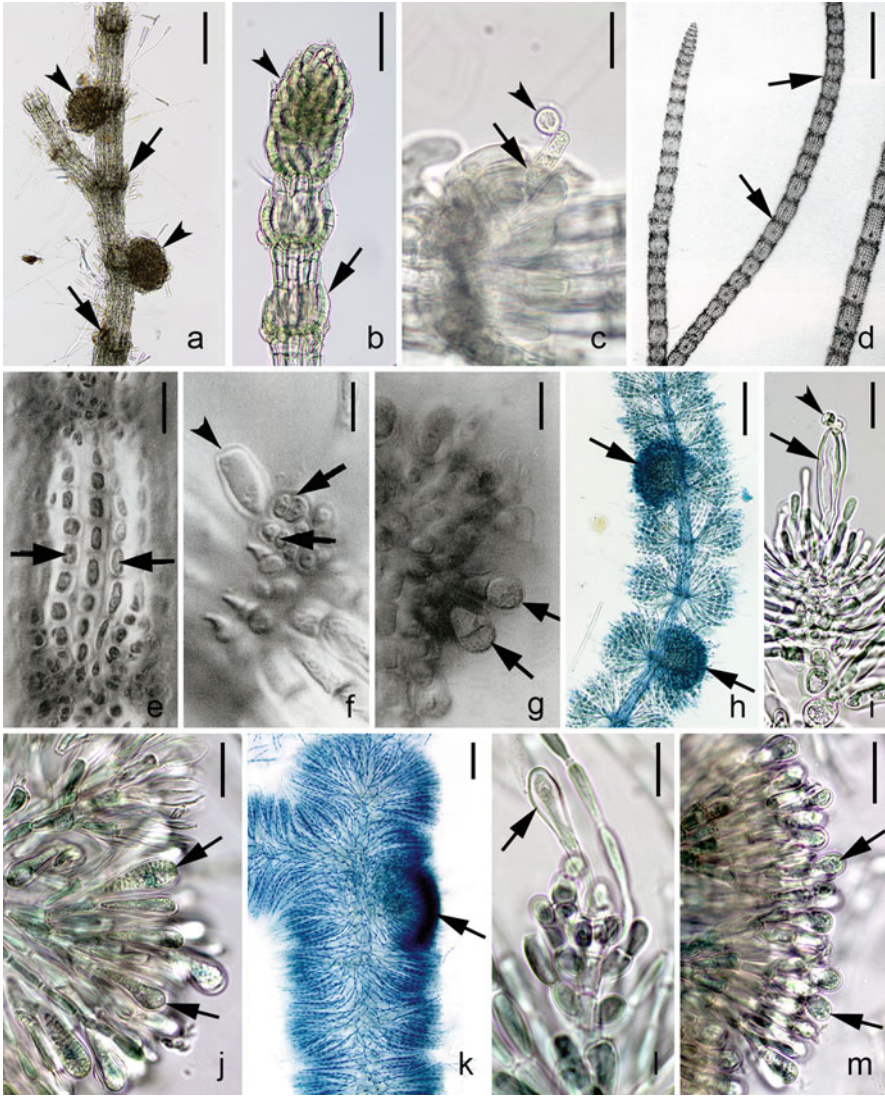
**Basionym:** *Batrachospermum latericum* Entwisle and Foard, Muelleria 11: 28 (1998).

**Type:** MEL2277053, TJ Entwisle #2507, 4.iii.1996 (Holotype).

**Type locality:** Australia, Tasmania, Southwest National Park, Old River, 43.3114° S, 146.2453° E.

**Description:** thalli monoecious, olive green; whorls reduced, 99–180  $\mu\text{m}$  in diameter; primary fascicles unbranched, 2–4 barrel-shaped or obovoidal cells; secondary fascicles present, one-celled; spermatangia  $\sim 8$   $\mu\text{m}$  in diameter; carpogonial branches 1–2 cells; carpogonia 22–24  $\mu\text{m}$  in length with fusiform to clavate trichogynes, 7–10  $\mu\text{m}$  in diameter; carposporophytes hemispherical, 1 per whorl,  $\sim 160$   $\mu\text{m}$  in diameter; carposporangia obovoidal or spherical 20–26  $\mu\text{m}$  in length and 16–18  $\mu\text{m}$  in diameter.





**Fig. 5.46** (a–c) *Nothocladus diatyches*: (a) highly reduced whorls (arrows) with large axial carposporophytes (arrowheads); (b) fascicles adhering to the main axis (arrow) and overtopping the tip of the branch (arrowhead); (c) carpogonium protruding from the whorl with an ellipsoidal trichogyne (arrow) and attached spermatium (arrowhead); (d–g) *Nothocladus latericius*: (d) highly reduced whorls (arrows) providing a banded appearance; (e) cortical cells of the main axis rectangular to square (arrows); (f) involucre bracts (arrows) subtending a carpogonium with an clavate trichogyne (arrow); (g) carposporophyte with obovoidal carposporangia (arrows); (h–j) *Nothocladus theaquis*: (h) barrel-shaped whorls with large axial compact carposporophytes (arrows); (i) carpogonium with an clavate trichogyne (arrow) and attached spermatium (arrowhead); (j) carposporophyte with ellipsoidal carposporangia (arrows); (k–m) *Nothocladus verruculosus*: (k) barrel-shaped contiguous whorls with large loosely arranged carposporophyte (arrow); (l) carpogonium with an clavate trichogyne (arrow); (m) carposporophyte with obovoidal carposporangia (arrows); Scale bars: (a, h, k) = 100  $\mu\text{m}$ ; (b) = 50  $\mu\text{m}$ ; (c, e, g, i, j, l, m) = 20  $\mu\text{m}$ ; (d) = 1000  $\mu\text{m}$ ; (f) = 10  $\mu\text{m}$  (Fig. (d–g) reprinted with permission by the Royal Botanical Gardens from Entwisle and Foard (1998))

**Diagnostic characters:** this species can be distinguished from *N. theaquus* and *N. verruculosus* based on reduced rather than well-developed whorls; it differs from *N. diatyches* in having shortercelled fascicles and the thallus apical cell protruded.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle and Foard (1998), Entwisle et al. (2016).

*Nothocladus theaquus* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:392 (2016) (Fig. 5.46h–j)

**Basionym:** *Batrachospermum theaquum* Entwisle and Foard, Austral Syst Bot 10: 357 (1997).

**Type:** NSW287958, AHS Lucas, i.1913 (Holotype).

**Type locality:** Australia, New South Wales, Middle Harbour, Gordon, 33.7300° S, 151.1500° E (estimated).

**Description:** thalli dioecious or monoecious, olive-green; whorls sub-spherical, barrel- or disc-shaped, contiguous, 360–550(–1600) µm in diameter; primary fascicles 9–13(–30) cells, proximal cells ellipsoidal, distal cells obovoidal; secondary fascicles abundant; spermatangia 5–8 µm in diameter; carpogonial branches 3–6 cells; carpogonia 38–75 µm in length with fusiform, ellipsoidal to elongate clavate trichogynes, 7–11 µm in diameter; carposporophytes spherical, 1 (–2) per whorl, 200–300 µm in diameter; carposporangia obovoidal, 13–15 µm in length and 12–13 µm in diameter.

**Diagnostic characters:** this species can be distinguished from *N. diatyches* and *N. latericius* based on well-developed rather than reduced whorls; it has compact, spherical carposporophytes whereas as *N. verruculosus* has semispherical, loosely arranged carposporophytes.

**Representative sequences in GenBank:** KT802763 (COI-5P); KT802861, KT802862, KT802863 (*rbcL*).

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

**Remarks:** there can be considerable variation in morphology between the New South Wales and Tasmanian populations and this is detailed in Entwisle et al. (2016). This species was reported from China (Xie et al. 2020), but this record would need to be verified with DNA sequence data as it is unlikely to occur outside of Australasia.

*Nothocladus verruculosus* Entwisle and ML Vis, J Phycol 52:393 (2016) (Fig. 5.46k–m)

**Type:** NSW747866, TJ Entwisle #3366, 5.vii.2007 (Holotype).

**Type locality:** Australia, Southwest Tasmania, at start of Lake Judd track, Scotts Peak Dam Rd, Red Tape Creek, 43.0186° S, 146.3658° E.

**Description:** thalli monoecious, gray-green to red-brown; whorls sub-spherical, barrel- or disc-shaped, contiguous, 120–300 µm in diameter; primary fascicles

7–8 cells, proximal cells ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia ~5 µm in diameter; carpogonial branches 2–6 cells; carpogonia 40–65 µm in length with stalked fusiform to elongate-clavate trichogynes, 3–6 µm in diameter; carposporophytes axial, semispherical, loosely arranged, 1 per whorl, 140–150 µm in diameter; gonimoblast filaments 4–6 cells; carposporangia obovoidal, 9.3–15.2 µm in length and 7.3–9 µm in diameter.

**Diagnostic characters:** this species can be distinguished from *N. diatyches* and *N. latericius* based on well-developed rather than reduced whorls; it has semispherical, loosely arranged carposporophytes whereas *N. theaquus* has compact, spherical carposporophytes.

**Representative sequences in GenBank:** KT802764 (COI-5P); AY297050, KT802864, KT802865 (*rbcL*).

**Distribution:** Australasia: Australia, New Zealand (Fig. 5.42).

**Key references:** Skuja (1934), Entwisle et al. (2016).

Key to species not assigned to a section

1a	Carposporophytes pedunculate	2
1b	Carposporophytes axial	3
2a	Carposporophyte compact, carposporangia large ( $\geq 30 \times 18 \mu\text{m}$ )	<i>N. antiquus</i>
2b	Carposporophyte loosely arranged; carposporangia small ( $< 18 \times 10 \mu\text{m}$ )	<i>N. debilis</i>
3a	Carposporophytes with determinate gonimoblast filaments only	<i>N. prominens</i>
3b	Carposporophytes with determinate and indeterminate gonimoblast filaments	<i>N. terawhiticus</i>

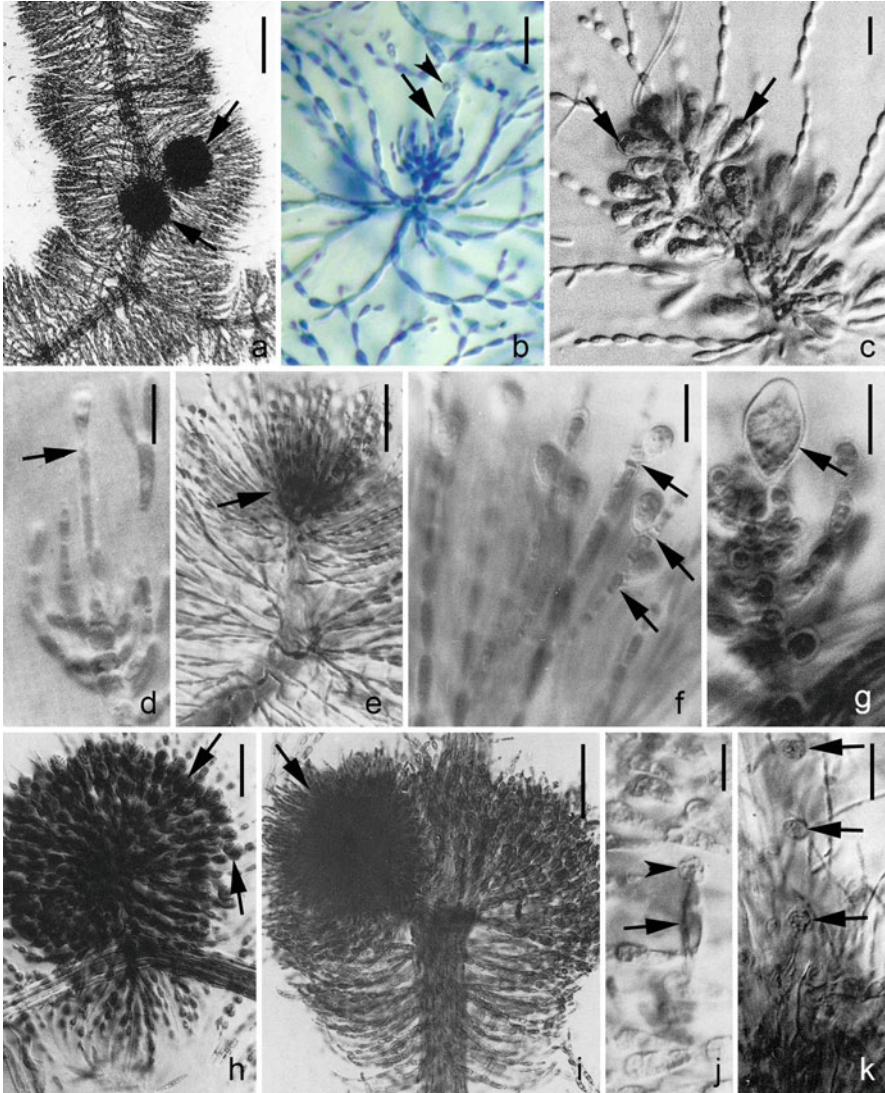
*Nothocladus antiquus* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:394 (2016) (Fig. 5.47a–c)

**Basionym:** *Batrachospermum antiquum* Entwisle and Foard, Austral Syst Bot 10: 348 (1997).

**Type:** MEL2033386A, TJ Entwisle #2508 and NG Walsh, 4.iii.1996 (Holotype).

**Type locality:** Australia, Tasmania, Southwest National Park, Bathurst Harbour, Old River, 43.3114° S, 146.2453° E.

**Description:** thalli monoecious, grass-green, mucilaginous; whorls barrel- or disc-shaped, contiguous, 400–500 µm in diameter; main axis covered by cylindrical cells; primary fascicles 7–12 cells, proximal cells ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia 5–6 µm in diameter; carpogonial branches 4–6 cells; carpogonia 44–53 µm in length with stalked ellipsoidal to clavate trichogynes sometimes with basal protuberance, 10–16 µm in diameter; carposporophytes short pedunculate, spherical, compact, 1(–2) per whorl, gonimoblast filaments 1–2 cells, 120–175 µm in diameter; carposporangia obovoidal, or elongate obovoidal 30–45 µm in length and 18–20 µm in diameter.



**Fig. 5.47** (a–c) *Nothocladus antiquus*: (a) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (b) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatia (arrowhead); (c) carposporophyte with obovoidal carposporangia (arrows); (d–f) *Nothocladus debilis*: (d) carpogonium with elongate cylindrical trichogyne (arrow); (e) pedunculate, loosely arranged carposporophyte (arrow); (f) carposporophyte with obovoidal carposporangia (arrows) produced laterally on gonimoblast filaments; (g, h) *Nothocladus prominens*: (g) carpogonium with inflated clavate trichogyne (arrowhead); (h) spherical, axial carposporophyte with obovoidal carposporangia (arrows); (i–k) *Nothocladus terawhiticus*: (i) pear-shaped whorl with large, spherical carposporophyte (arrow); (j) fertilized carpogonium with fusiform trichogyne (arrowhead) and attached spermatium (arrowhead); (k) carposporophyte with indeterminate gonimoblast filament producing carposporangia (arrows). Scale bars: (a) = 150 µm; (b, c, h) = 25 µm; (d, g, j) = 15 µm; (e, i) = 100 µm; (f) = 20 µm; (k) = 50 µm (Image author: Fig. (b) T Entwisle. Fig. (a, c–k) reprinted with permission by CSIRO Publishing from Entwisle and Foard (1997))



**Diagnostic characters:** this species is distinguished based on the combination of compact carposporophytes, large carposporangia, and short gonimoblast filaments.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus debilis* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52:394 (2016) (Fig. 5.47d–f)

**Basionym:** *Batrachospermum debilis* Entwisle and Foard, Austral Syst Bot 10: 362 (1997).

**Type:** MEL2033517, TJ Entwisle #2566 and NG Walsh, 8.iii.1996 (Holotype).

**Type locality:** Australia, Tasmania, Southwestern National Park, Mount Rugby, Creek into Bathurst Narrows, 43.3489° S, 146.1164° E.

**Description:** thalli monoecious, green to dark brown; mucilaginous; whorls barrel- or disc-shaped, contiguous, 300–550 µm in diameter; main axis covered in cylindrical cells; primary fascicles 6–12 cells, proximal cells ellipsoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia 5–6 µm in diameter; carpogonial branches 5–7 cells; carpogonia 32–60 µm in length with sessile clavate or elongate cylindrical trichogynes, 3–5 µm in diameter; carposporophytes pedunculate, semispherical, loosely arranged, 1 per whorl, 160–200 µm in diameter; gonimoblast filaments 4–11 cells; carposporangia obovoidal, 10–16 µm in length and 7–9 µm in diameter.

**Diagnostic characters:** this species is distinguished by carposporophytes loosely arranged, long gonimoblast filaments with a lateral series of carposporangia.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus prominens* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52: 394 (2016) (Fig. 5.47g, h)

**Basionym:** *Batrachospermum prominens* Entwisle and Foard, Austral Syst Bot 10: 368 (1997).

**Type:** MEL2020289, TJ Entwisle #2390, 5.i.1994 (Holotype).

**Type locality:** Australia, Western Australia, Fernhook Falls, Deep River, 34.8917° S, 116.4833° E.

**Description:** thalli dioecious, grass-green, mucilaginous; whorls barrel- or disc-shaped, contiguous to separate, 200–250 µm in diameter; main axis covered in cylindrical cells; primary fascicles 4–6 cells, proximal cells ellipsoidal, distal cells ellipsoidal to sub-spherical; secondary fascicles abundant; spermatangia 7–8 µm in diameter; carpogonial branches 3–5 cells; carpogonia 35–40 µm in length with sessile ellipsoidal trichogynes, 8–13 µm in diameter; carposporophytes axial, spherical, loosely arranged, 1 per whorl, higher than the whorl, 160–300 µm in

diameter; gonimoblast filaments 2–5 cells; carposporangia obovoidal or ellipsoidal, 22–34 µm in length and 19–22 µm in diameter.

**Diagnostic characters:** this species is distinguished based on axial carposporophytes composed of determinate gonimoblast filaments.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: Australia (Fig. 5.42).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

*Nothocladus terawhiticus* (Entwisle and Foard) Entwisle and ML Vis, J Phycol 52: 394 (2016) (Fig. 5.47i–k)

**Basionym:** *Batrachospermum terawhiticum* Entwisle and Foard, Austral Syst Bot 10:371 (1997).

**Type:** AKU101795, VW Lindauer #1185, 24.x.1938 (Holotype).

**Type locality:** New Zealand, North Island, Bay of Islands, Te Rawhiti Creek, 38.55° S, 175.3166667° E.

**Description:** thalli monoecious, red or purple when dry, mucilaginous; whorls pear-shaped, separate or contiguous, 232–437 µm in diameter; primary fascicles 6–10 cells, proximal cells cylindrical to ellipsoidal, obovoidal, distal cells ellipsoidal to obovoidal; secondary fascicles abundant; spermatangia 5–7 µm in diameter; carpogonial branches 6–11 cells; carpogonia 23–42 µm in length with sessile cylindrical to clavate trichogynes, 5–8 µm in diameter; carposporophytes axial, spherical, compact, 1–2 per whorl, 90–232 µm in diameter; gonimoblast with determinant 2–8 cells and indeterminate filaments; carposporangia obovoidal, spherical, 18–31 µm in length and 11–18(–22) µm in diameter.

**Diagnostic characters:** this species is distinguished based on large carposporophytes with both determinate and indeterminate gonimoblast filaments. In this respect, it is similar to species of *Paludicola* treated in other part of this book.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Australasia: New Zealand (Fig. 5.42).

**Key references:** Entwisle and Foard (1997), Entwisle et al. (2016).

## Genus *Paludicola*

*Paludicola* Necchi and MLVis, J Phycol 56:852 (2020b)

**Synonyms:** section *Turfosa* Sirodot, CR Acad Sci 76:1219 (1873); section “Turficoles” Sirodot, Les Batrachospermes, 259 (1884); section *Turficola* De Toni, Sylloge Floridearum, 58 (1897a); section *Turficola* De Toni emend. Necchi, Bibl Phycol 84:124 (1990).

**Type species:** *P. turfosa* (Bory) ML Vis and Necchi, J Phycol 56:854 (2020b).

**Description:** plants monoecious, dioecious, or polyecious, greenish, greenish-blue, or brownish, consistency mucilaginous; branching pseudodichotomous or



irregular in few species; whorls well developed or reduced, contiguous, obconic, pear-shaped, barrel-shaped, or compressed and indistinct; cortical filaments of the main axis well developed with cylindrical cells, loosely arranged or detached from the axial cells; primary fascicles straight, dichotomous- or trichotomously branched, or curved, unilaterally branched, formed by cells variable in shape and length along the fascicle, ranging from cylindrical to ellipsoidal, obovoidal or pear-shaped or audouinelloid, with cylindrical or barrel-shaped cells; secondary fascicles abundant and covering half or the entire internode; spermatangia on primary or secondary fascicles, in some species predominantly on secondary fascicles or forming dense clusters; carpogonial branches well differentiated from the fascicles, straight or less often slightly curved, composed of barrel- or disc-shaped cells, developing from the periaxial or proximal cells of primary fascicles, rarely from secondary fascicles or cortical filaments, short, composed of disc- or barrel-shaped cells; involucrel filaments, short, composed of barrel-shaped or spherical cells, usually forming a knot around carpogonium; carpogonia with unstalked, rarely stalked, clavate trichogynes; carposporophytes axial, hemispherical or ovoidal, inserted within the whorls, 1, rarely 2, per whorl, large; gonimoblast filaments of two types: radially branched, densely or loosely arranged, determinate with ellipsoidal, cylindrical, or barrel-shaped cells and diffuse, indeterminate with cylindrical cells, prostrate, creeping around fascicles and on cortical filaments; carposporangia obovoidal, ellipsoidal, sub-spherical, spherical, or clavate; monosporangia occur in few species, on primary or secondary fascicles, obovoidal, spherical, or sub-spherical.

**Diagnostic characters:** the genus is characterized by having carpogonia with unstalked, rarely stalked, and clavate trichogynes; and gonimoblast filaments of two types: radially branched, densely or loosely arranged, determinate with ellipsoidal, cylindrical, or barrel-shaped cells; and diffuse, and indeterminate with cylindrical cells, prostrate, creeping around fascicles and on cortical filaments.

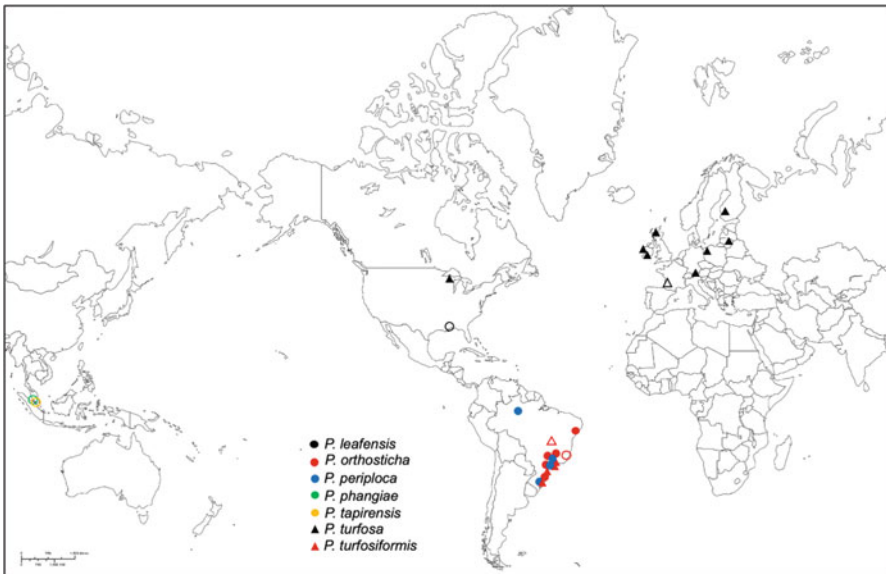
**Habitat:** species of *Paludicola* typically occur in waters with acidic to slightly acidic pH (pH 4.2–6.7), yellow to dark brown color, less often in clear waters, low ion content (conductivity 15–58  $\mu\text{S cm}^{-1}$ ), low to moderate temperatures (7–15 °C, less often above 20 °C) and still to moderately flowing waters, ponds, or springs, attached to macrophytes or rocky substrata, in open or partly shaded stream segments (Sheath et al. 1994c; Eloranta et al. 2016; Eloranta 2019).

**Distribution:** representatives of the genus have been reported in temperate or sub-tropical, less often in tropical regions, of Asia, Europe, North and South America (Figs. 5.48 and 5.49).

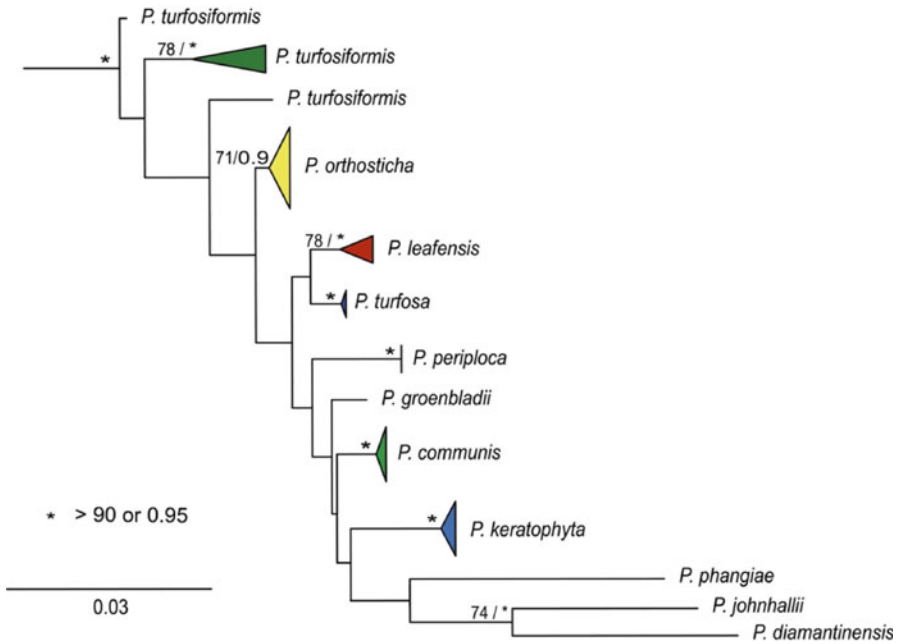
**Phylogenetic relationships among species:** analyses of the *rbcL* sequences within the genus (Fig. 5.50) based on data reported by Vis et al. (2020b) showed seven species in distinct clades (*P. communis*, *P. groenbladii*, *P. keratophyta*, *P. leafensis*, *P. orthosticha*, *P. periploca*, and *P. turfosa*) and three species on long branches (*P. diamantinensis*, *P. johnhallii*, and *P. phangiae*). The three latter species are exceptions in the group by having irregular instead of pseudodichotomous branching. *Paludicola turfosisiformis* was paraphyletic in



**Fig. 5.48** World map showing the distribution of the following species of *Paludicola*: *P. aquanigra*, *P. bakarensis*, *P. communis*, *P. diamantinensis*, *P. gombakensis*, *P. groenbladii*, *P. johnhallii*, and *P. keratophyta*. Open symbols represent the type localities



**Fig. 5.49** World map showing the distribution of the following species of *Paludicola*: *P. leafensis*, *P. orthosticha*, *P. periploca*, *P. phangiae*, *P. tapirensis*, *P. turfosa*, and *P. turfosisformis*. Open symbols represent the type localities



**Fig. 5.50** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Paludicola*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

single gene analyses but was monophyletic in the concatenated analyses of *rbcL* and COI-5P (Vis et al. 2020b), which also showed *P. aquanigra* (with COI-5P sequence only) as a distinct species. There are three species without sequence data (*P. bakarensis*, *P. gombakensis*, and *P. tapirensis*) that are distinguished by morphology.

Key to the species of the genus *Paludicola*

1a	Whorls composed of curved fascicles, unilaterally branched	2
1b	Whorls composed of straight fascicles, dichotomous- or trichotomously branched	4
2a	Fascicles composed of audouinelloid cells (cylindrical or barrel-shaped)	<i>P. gombakensis</i>
2b	Fascicles composed of non-audouinelloid cells	3
3a	Spermatangia on secondary fascicles, rarely on primary fascicles, carpogonial branches and trichogynes straight	<i>P. orthosticha</i>
3b	Spermatangia on primary or secondary fascicles, carpogonial branches, and trichogynes curved	<i>P. bakarensis</i>
4a	Spermatangia arranged in dense clusters	<i>P. aquanigra</i>
4b	Spermatangia not arranged in dense clusters	5
5a	Branching irregular, carposporophytes loose	6

(continued)

5b	Branching pseudodichotomous, carposporophytes dense or loose	8
6a	Carposporophytes typically lower than whorls	<i>P. phangiae</i>
6b	Carposporophytes typically higher than whorls	7
7a	Carposporangia large ( $\geq 16 \mu\text{m}$ in length and $\geq 14 \mu\text{m}$ in diameter)	<i>P. diamantinensis</i>
7b	Carposporangia small ( $\leq 15 \mu\text{m}$ in length and $\leq 10 \mu\text{m}$ in diameter)	<i>P. johnhallii</i>
8a	Spermatangia on secondary fascicles, rarely on primary fascicles	<i>P. periploca</i>
8b	Spermatangia indistinctly on primary or secondary fascicles	9
9a	Mature carposporophytes present	10
9b	Mature carposporophytes not observed	11
10a	Carposporophytes loose, indistinguishable from whorls, trichogynes curved	<i>P. tapirensis</i>
10b	Carposporophytes dense, clearly distinguishable from whorls, trichogynes, straight	<i>P. turfosisiformis</i>
11a	Known distribution primarily in Europe	12
11b	Known distribution primarily in North America	13
12a	Whorls well developed or less often reduced	<i>P. keratophyta</i> <sup>a</sup>
12b	Whorls reduced	<i>P. groenbladii</i> <sup>a</sup> and <i>P. turfosa</i> <sup>a</sup>
13a	Whorls typically reduced or less often well developed, widely distributed	<i>P. communis</i> <sup>a</sup>
13b	Whorls reduced, known from the type locality only	<i>P. leafensis</i> <sup>a</sup>

<sup>a</sup>These species are unequivocally distinguished only based on DNA sequence data

***Paludicola aquanigra*** Necchi and ML Vis, J Phycol 56:856 (2020b) (Fig. 5.51a–e)

**Type:** SJRP 32596, O Necchi Jr & CC Necchi, 2.vii.2018 (Holotype).

**Type locality:** Brazil: Bahia, Palmeiras, National Park of Chapada Diamantina, trail to the higher part of “Cachoeira da Fumaça,” 12.60388889° S, 41.46638889° W.

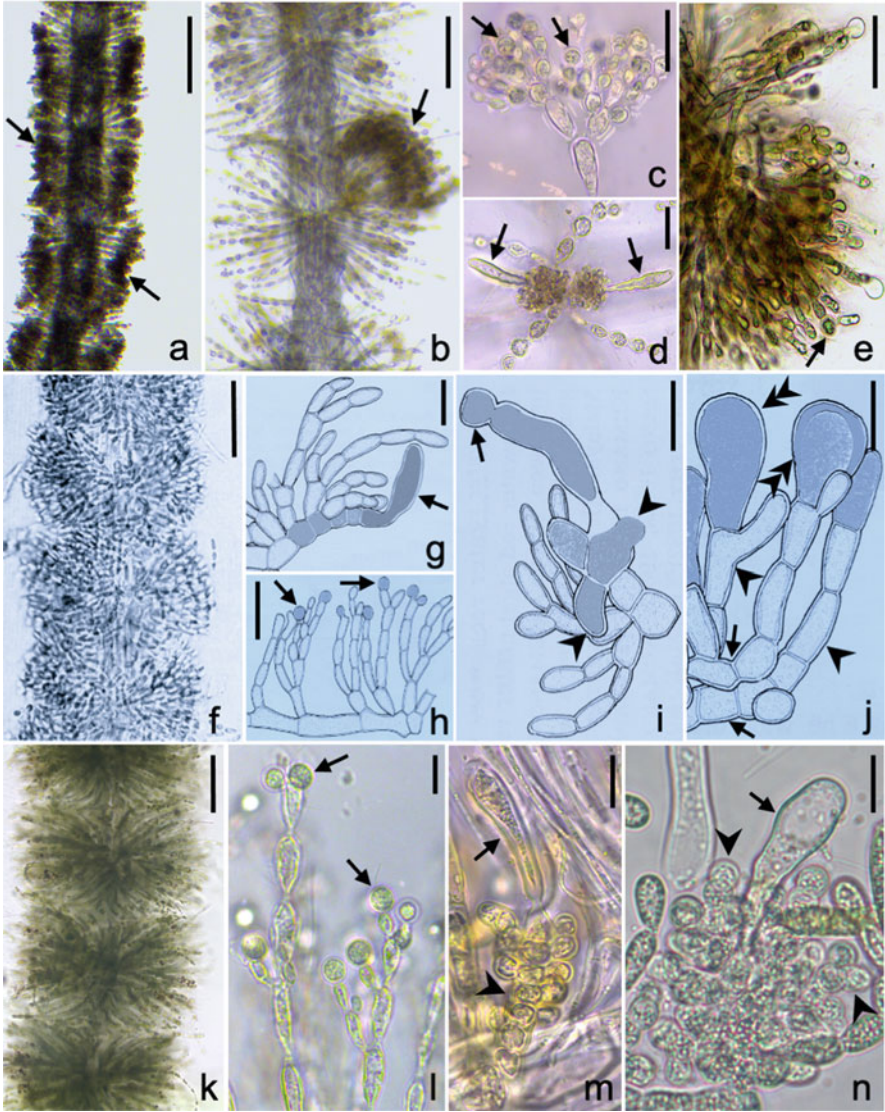
**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical or compressed and indistinct, 205–360  $\mu\text{m}$  in diameter; primary fascicles straight, with 4–7 cells; secondary fascicles abundant, covering half to the entire internode; spermatangia on primary or secondary fascicles, forming dense clusters, 6–8  $\mu\text{m}$  in diameter; carpogonial branches straight, composed of 3–6 cells, developing from the periaxial, rarely from proximal cells of primary fascicles, 19–30  $\mu\text{m}$  in length; carpogonia 51–63  $\mu\text{m}$  in length, 8–11  $\mu\text{m}$  in diameter; carposporophytes dense, higher than whorls, 150–255  $\mu\text{m}$  in diameter, 105–150  $\mu\text{m}$  in height; carposporangia obovoidal or sub-spherical, 15–19  $\mu\text{m}$  in length and 11–14  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is unique in the genus in having spermatangia arranged in dense clusters on primary or secondary fascicles.

**Representative sequences in GenBank:** MN943950 (COI-5P).

**Distribution:** South America: Brazil (Fig. 5.48).

**Key reference:** Vis et al. (2020b).



**Fig. 5.51** (a–d) *Paludicola aquanigra*: (a) reduced whorls with dense clusters of spermatangia (arrows); (b) whorls with loose carposporophyte (arrow); (c) spermatangia (arrows) in dense clusters on primary fascicle; (d) two mature carpogonia with clavate trichogynes (arrows); (e) gonimoblast filaments with carposporangium (arrow); (f–j) *Paludicola bakarensis*: (f) reduced whorls; (g) mature carpogonium with clavate trichogyne (arrow); (h) spermatangia (arrows) on primary and secondary fascicles; (i) fertilized carpogonium with attached spermatium (arrow) and initial gonimoblast filaments (arrowheads); (j) prostrate (arrows) and erect (arrowheads) gonimoblast filaments with carposporangia (double arrowheads); (k–n) *Paludicola communis*: (k) reduced whorls; (l) spermatangia (arrows) on primary and secondary fascicles; (m) carpogonium with clavate trichogyne (arrow) and carpogonial branch (arrowhead); (n) carpogonium with clavate trichogyne (arrow) and involucre filaments (arrowheads). Scale bars: (a) = 200 μm; (b, f, k) = 100 μm; (e, h) = 50 μm; (c, d) = 25 μm; (g, i, j, l–n) = 10 μm (Fig. (f–j) redrawn from Kumano and Ratnasabapathy (1984))



*Paludicola bakarensis* (Kumano and Ratnasabapathy) Necchi and MLVis, J Phycol 56:858 (2020b) (Fig. 5.51f–j)

**Basionym:** *Batrachospermum bakarensis* Kumano and Ratnasabapathy, Jap J Phycol. 32:20 (1984).

**Type:** TNS-AL 169079, M Ratnasabapathy no.13, 03.vi.1982 (Holotype); KLU, TNS-AL 169085 (Isotypes).

**Type locality:** Malaysia, Kelantan, Sungai Bakar, 05.829413° N, 102.226938° E.

**Description:** plants dioecious; branching irregular; whorls reduced, contiguous, barrel-shaped, 100–300 µm in diameter; primary fascicles curved, unilaterally branched, with 4–7(–9) cells; secondary fascicles abundant and covering the entire internode; spermatangia on primary or secondary fascicles, 4–6 µm in diameter; carpogonial branches slightly curved, composed of 2–5 cells, developing from the periaxial or proximal cells of primary fascicles, 12–30 µm in length; carpogonia with curved trichogynes, 23–36 µm in length, 6–10 µm in diameter; carposporophytes dense, lower than whorls, 80–120 µm in diameter and 40–80 µm in height; carposporangia clavate or obovoidal, 13–18 µm in length and 7–10 µm in diameter.

**Diagnostic characters:** this species is unique in the genus due to the presence of curved and unilaterally branched primary and secondary fascicles, slightly curved carpogonial branches and trichogynes and dense carposporophytes that are lower than whorls.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia (Fig. 5.48).

**Key references:** Kumano and Ratnasabapathy (1984), Kumano (2002), Vis et al. (2020b).

*Paludicola communis* ML Vis and Necchi, J Phycol 56:855 (2020b) (Fig. 5.51k–n)

**Type:** BHO A-0191, ML Vis and ET Johnston, 12.viii.2010 (Holotype, Isotypes MICH 1210865, SJRP 32598).

**Type locality:** the USA: New Hampshire, Ossipee River, 43.925556° N, 71.04° W,

**Description:** plants monoecious; branching pseudodichotomous; whorls typically reduced but can be well developed in some populations, contiguous, barrel-shaped or compressed and indistinct, 210–380(–515) µm in diameter; primary fascicles straight, with 4–8(–11) cells; secondary fascicles abundant and covering half to the entire internode; spermatangia on primary or secondary fascicles, 6–8 µm in diameter; carpogonial branches straight, composed of (3–)4–7 cells, developing from the periaxial cells, 20–37 µm in length; carpogonia 33–48 µm in length, 7.5–11(–14.5) µm in diameter; carposporophytes and carposporangia not observed.

**Diagnostic characters:** this species is morphologically similar to *P. keratophyta* and *P. turfosa*, that occur primarily in Europe, and can be unequivocally distinguished based only on DNA sequence data.

**Representative sequences in GenBank:** EU636746, MN943962 (COI-5P), AY423408, MN943925 (*rbcL*).



**Distribution:** North America: Canada, Costa Rica, the USA; South America: French Guiana (Fig. 5.48).

**Key reference:** Vis et al. (2020b).

*Paludicola diamantinensis* Necchi and ML Vis, J Phycol 56:856 (2020b) (Fig. 5.52a–d)

**Type:** SJRP 32597, O Necchi Jr and CC Necchi, 2.vii.2018 (Holotype).

**Type locality:** Brazil: Bahia, Capão Valley, Riachinho Stream, 12.57222222° S, 41.51472222° W.

**Description:** plants dioecious; branching irregular; whorls well developed, contiguous, obconical or compressed and indistinct, 295–475 µm in diameter; primary fascicles straight, with 8–12 cells; secondary fascicles abundant, covering half of the internode; spermatangia on primary or secondary fascicles, forming dense clusters, 5–8 µm in diameter; carpogonial branches straight, composed of 4–6(–10) cells, developing from the periaxial, rarely from proximal cells of primary fascicles, 19–33(–53) µm in length; carpogonia 41–66 µm in length, 10–16 µm in diameter; carposporophytes loose, higher or as high as whorls, 190–363 µm in diameter, 75–170 µm in height; carposporangia obovoidal or sub-spherical, 16–22.5 µm in length and 14–16.5 µm in diameter.

**Diagnostic characters:** this species is distinguishable from the other species in the genus by the following combination of characters: irregular branching, well-developed whorls, loose carposporophytes that are higher or the same height of whorls and large carposporangia ( $\geq 16$  µm in length and  $\geq 14$  µm in diameter).

**Representative sequences in GenBank:** MN943969 (COI-5P), MN943927 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.48).

**Key reference:** Vis et al. (2020b).

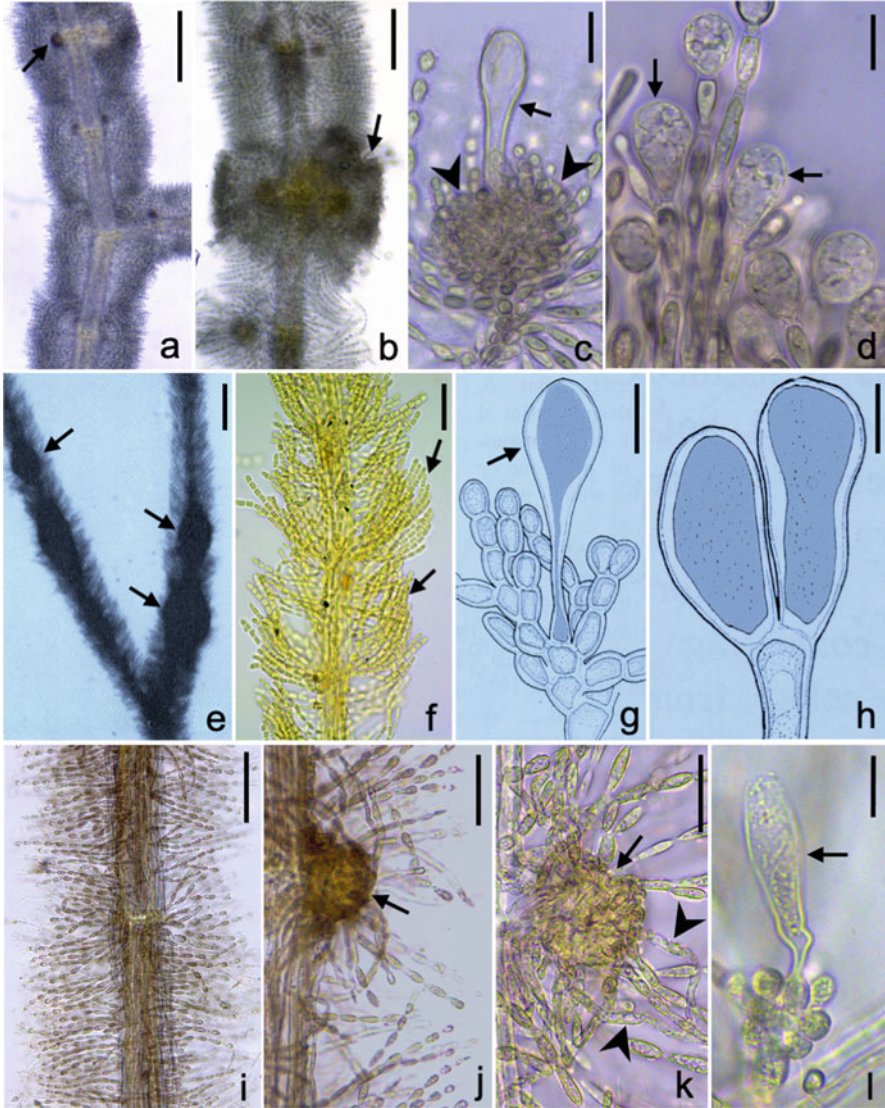
*Paludicola gombakensis* (Kumano and Ratnasabapathy) ML Vis and Necchi, J Phycol 56:858 (2020b) (Fig. 5.52e–h)

**Basionym:** *Batrachospermum gombakense* Kumano and Ratnasabapathy in Ratnasabapathy and Kumano, Jap J Phycol 30:119 (1982b).

**Type:** KLU, M Ratnasabapathy no.1220, 31.v.1976 (Holotype); TNS-AL 169097 (Isotype).

**Type locality:** Malaysia, Selangor, Sungai Gombak, 03.238221° N, 101.716028° E.

**Description:** plants dioecious; branching pseudodichotomous; whorls well developed, contiguous, compressed and indistinct, 200–400 µm in diameter; primary fascicles curved, unilaterally branched, audouinelloid, with 9–15 cells; secondary fascicles abundant and covering the entire internode; spermatangia 4–8 µm in diameter, on primary or secondary fascicles; carpogonial branches straight, composed of 1–3 cells, developing from the periaxial cells, 5–15 µm in length; carpogonia 40–50 µm in length, 10–15 µm in diameter; carposporophytes dense, lower than whorls, 185–330 µm in diameter, 140–210 µm in height; carposporangia obovoid or clavate, 20–25 µm in length, 8–11 µm in diameter.



**Fig. 5.52** (a–d) *Paludicola diamantinensis*: (a) well-developed whorls with a knot of carpogonia (arrows); (b) whorls with loose carposporophyte (arrow); (c) mature carpogonium with clavate trichogyne (arrow) and involucre filaments (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Paludicola gombakensis*: (e) compressed and well-developed whorls with carposporophytes (arrows); (f) whorls with curved and audouinelloid fascicles (arrows); (g) mature carpogonium with clavate trichogyne (arrow); (h) carposporangia terminal on gonimoblast filaments; (i–l) *Paludicola groenbladii*: (i) compressed and reduced whorls; (j) immature or aborted carposporophyte with a knot of gonimoblast filaments (arrow); (k) immature or aborted carposporophyte with a knot of gonimoblast filaments (arrow) and prostrate gonimoblast filament (arrowhead); (l) mature carpogonium with clavate trichogyne (arrow). Scale bars: (a, e) = 200 µm; (b, i) = 100 µm; (f, j, k) = 50 µm; (c, d, g, l) = 10 µm; (h) = 5 µm (Fig. (e, g, h) redrawn from Kumano (2002) and Ratnasabapathy and Kumano (1982b))

**Diagnostic characters:** this species is distinguishable from other species in the genus by the combination of curved and unilaterally branched primary fascicles with audouinelloid cells, dense carposporophytes that are lower than whorls and large carposporangia ( $\geq 20$   $\mu\text{m}$  in length).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia (Fig. 5.48).

**Key references:** Ratnasabapathy and Kumano (1982b), Kumano (2002), Vis et al. (2020b).

*Paludicola groenbladii* ML Vis, Necchi and P Eloranta, J Phycol 56:855 (2020b) (Fig. 5.52i–l)

**Type:** BHO A-1525, P Eloranta, 22.vii.2011 (Holotype; Isotypes HU; SJRP 32599).

**Type locality:** Finland: Mänttä-Vilppula, Lake Saukkolampi, 62.2397° N, 24.1642° E.

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical or compressed and indistinct, 310–415  $\mu\text{m}$  in diameter; primary fascicles straight, with 4–8 cells; secondary fascicles abundant and covering half to the entire internode; spermatangia on primary or secondary fascicles, 7–10  $\mu\text{m}$  in diameter; carpogonial branches straight, composed of (2–)4–8 cells, developing from the periaxial cells, 17–37  $\mu\text{m}$  in length; carpogonia 39–50.5  $\mu\text{m}$  in length, 8–12.5  $\mu\text{m}$  in diameter; carposporophytes immature or potentially aborted; carposporangia not observed.

**Diagnostic characters:** this species is morphologically similar to *P. keratophyta* and *P. turfosa*, both occurring primarily in Europe, the latter overlapping in distribution; they can be unequivocally distinguished based only on DNA sequence data.

**Representative sequences in GenBank:** MN943971 (COI-5P), MN943929 (*rbcL*).

**Distribution:** Europe: Finland, Poland (Fig. 5.48).

**Key reference:** Vis et al. (2020b).

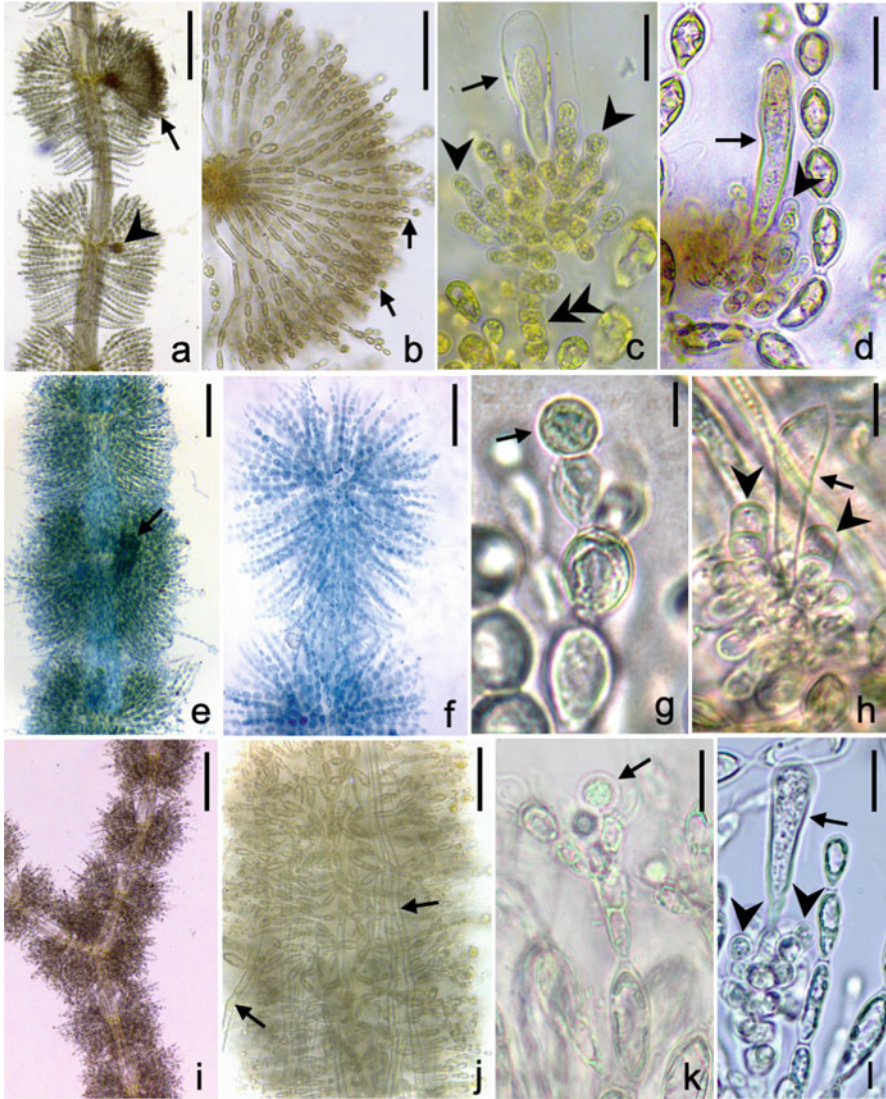
*Paludicola johnhallii* ML Vis and Necchi, J Phycol 56:855 (2020b) (Fig. 5.53a–d)

**Type:** BHO A-0198, JD Hall, 15.v.2010 (Holotype); MARY1010607, NY02143755, SJRP 32600 (Isotypes).

**Type locality:** the USA: New York, Ulster County, Minewaska State Park, Lake Awosting, 41.7032° N, 74.2941° W.

**Description:** plants dioecious; branching irregular; whorls well developed, contiguous, barrel-shaped, obconical or compressed and indistinct, 345–575  $\mu\text{m}$  in diameter; primary fascicles straight, with (8–)10–14 cells; secondary fascicles abundant, covering the entire internode; spermatangia on primary or secondary fascicles, 6–8  $\mu\text{m}$  in diameter; carpogonial branches straight, composed of 6–9 cells, developing from the periaxial, rarely from proximal cells of primary fascicles, 23–47  $\mu\text{m}$  in length; carpogonia 45–60  $\mu\text{m}$  in length, 8–11  $\mu\text{m}$  in diameter; carposporophytes loose, higher or as high as whorls, 205–395  $\mu\text{m}$  in





**Fig. 5.53** (a–d) *Paludicola johnhallii*: (a) well-developed whorls with carposporophyte (arrow) and a knot of carpogonia (arrowhead); (b) loose carposporophyte with carposporangia (arrows); (c, d) mature carpogonia with clavate trichogynes (arrow), involucre filaments (arrowheads) and carpogonial branch (arrowhead); (e–h) *Paludicola keratophyta*: (e) well-developed whorls with immature or aborted carposporophyte (arrow); (f) well-developed obconical whorls; (g) spermatangium on primary fascicle (arrow); (h) mature carpogonium with clavate trichogyne (arrow) and involucre filaments (arrowheads); (i–l) *Paludicola leafensis*: (i) well-developed obconical whorls; (j) main axis with loosely arranged cortical filaments (arrows); (k) spermatangium on primary fascicle (arrow); (l) mature carpogonium with clavate trichogyne (arrow) and involucre filaments (arrowheads). Scale bars: (a, i) = 200  $\mu$ m; (b, e, f, j) = 100  $\mu$ m; (c, d) = 20  $\mu$ m; (h, k, l) = 10  $\mu$ m; (g) = 5  $\mu$ m (Fig. (i, j) reproduced with permission by Wiley from Vis et al. (2020b))

diameter, 115–215  $\mu\text{m}$  in height; carposporangia obovoidal or sub-spherical, 12–15  $\mu\text{m}$  in length and 8.5–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species most closely resemble *P. diamantinensis* in having irregular branching, well-developed whorls, loose carposporophytes but differs by the presence of smaller carposporangia ( $\leq 15$   $\mu\text{m}$  in length and  $\leq 10$   $\mu\text{m}$  in diameter); in addition, they are geographically disjunct with *P. johnhallii* occurring exclusively in North America and *P. diamantinensis* only in South America.

**Representative sequences in GenBank:** MN943973, MN943974 (COI-5P), MN943930, MN943931 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.48).

**Key reference:** Vis et al. (2020b).

*Paludicola keratophyta* (Bory) ML Vis and Necchi, J Phycol 56:854 (2020b) (Fig. 5.53e–h)

**Basionym:** *Batrachospermum keratophytum* Bory, Ann Mus Hist Nat 12:328 (1808b).

**Type:** PC 0591537, Herbarium Thuret (Holotype).

**Type locality:** France, Landes, Marensin, 43.675199° N, 1.025655° W.

**Description:** plants monoecious; branching pseudodichotomous; whorls well developed or reduced, contiguous, obconical, barrel-shaped or compressed and indistinct, 245–465  $\mu\text{m}$  in diameter; primary fascicles straight, with 5–12 cells; secondary fascicles abundant and covering the entire internode; spermatangia on primary or secondary fascicles, 5.5–8  $\mu\text{m}$  in diameter; carpogonial branches straight, composed of 3–6 cells, developing from the periaxial cells, 17.5–30  $\mu\text{m}$  in length; carpogonia 40–69  $\mu\text{m}$  in length, 78–12.5  $\mu\text{m}$  in diameter; carposporophytes immature or potentially aborted; carposporangia not observed; monosporangia present in some populations, obovoidal, 8–13  $\mu\text{m}$  in length, 7–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** specimens with reduced whorls of this species are morphologically similar to *P. groenbladii* and *P. turfosa*, both occurring primarily in Europe and partly overlapping in distribution; they can be unequivocally distinguished based only on DNA sequence data.

**Representative sequences in GenBank:** KM592951, KM592949 (COI-5P), KJ825960, KM593833 (*rbcL*).

**Distribution:** Europe: France, Portugal, Spain; South America: Brazil (Fig. 5.48).

**Key references:** Sheath et al. (1994c), Eloranta et al. (2011), Chiasson et al. (2014), Vis et al. (2020b).

**Remarks:** Sheath et al. (1994c) proposed a lectotype but that was not necessary due to an existing holotype.

*Paludicola leafensis* ML Vis and Necchi, J Phycol 56:855 (2020b) (Fig. 5.53i–l)

**Type:** BHO-A1648, ML Vis, WB Chiasson, JC Hodge and KV Lehmkuhl, 5. ix.2003 (Holotype); MICH 1210866 (Isotype).

**Type locality:** the USA: Mississippi, Rt. 57, 0.5 km north of Leaf, 31.043992° N, 88.801576° W.

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, barrel-shaped or compressed and indistinct, 375–550 µm in diameter; primary fascicles straight, with 4–8 cells; secondary fascicles abundant and covering the entire internode; spermatangia on primary or secondary fascicles, 5–7 µm in diameter; carpogonial branches straight, composed of 5–8(–16) cells, developing from periaxial or proximal cells of primary fascicle cells, 27–48 µm in length; carpogonia 32–41 µm in length, 6–9 µm in diameter; carposporophytes and carposporangia not observed.

**Diagnostic characters:** this species is morphologically similar to *P. communis*, that also occur in the USA, and can be unequivocally distinguished based only on DNA sequence data.

**Representative sequences in GenBank:** MN943981 (COI-5P), MN943934 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.49).

**Key reference:** Vis et al. (2020b).

*Paludicola orthosticha* (Skuja) Necchi and ML Vis, J Phycol 56:857 (2020b) (Fig. 5.54a–e)

**Basionym:** *Batrachospermum orthostichum* Skuja, Hedwigia 71:84 (1931).

**Type:** UPS:BOT:A-724541, O Conde, x.1928 (Holotype).

**Type locality:** Brazil, Espírito Santo, Santa Teresa, 19.91666667° S, 40.60000000° W.

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical, pear-shaped or compressed and indistinct, 80–300 µm in diameter; primary fascicles curved, unilaterally branched, with (2–)3–7 cells; secondary fascicles abundant and covering the entire internode; spermatangia on secondary fascicles, rarely on primary fascicles, 6–10 µm in diameter; carpogonial branches straight, composed of 2–8 cells, developing from the periaxial cells, rarely from proximal cells or cortical filaments, 12–37 µm in length; carpogonia 30–52 µm in length, 6–12 µm in diameter; carposporophytes dense, higher than whorls, 90–230 µm in diameter, 60–120 µm in height; carposporangia obovoidal, 10–14 µm in length, 7–11 µm in diameter.

**Diagnostic characters:** this species is distinguishable from other species in the genus by the combination of curved and unilaterally branched primary fascicles, spermatangia on secondary fascicles, dense carposporophytes that are higher than whorls and small carposporangia ( $\leq 14$  µm in length,  $\leq 11$  µm in diameter).

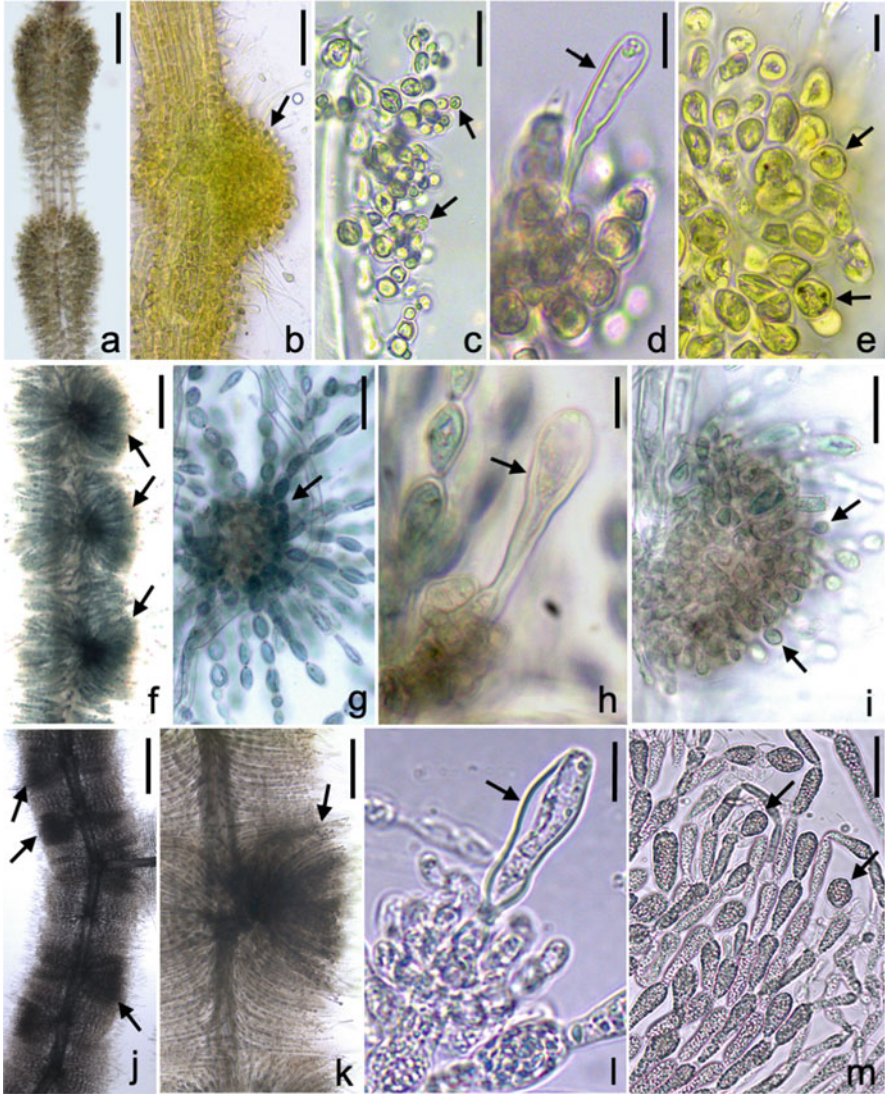
**Representative sequences in GenBank:** MN943982 (COI-5P), MN943937, MN943938 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.49).

**Key references:** Skuja (1931), Necchi (1990), Vis et al. (2020b).

*Paludicola periploca* (Skuja) Necchi and ML Vis, J Phycol 56:857 (2020b) (Fig. 5.54f–i)





**Fig. 5.54** (a–e) *Paludicola orthosticha*: (a) reduced elongate-obconical whorls; (b) axis with a dense carposporophyte (arrow); (c) spermatangia (arrows) on secondary fascicles (arrows); (d) mature carpogonium with clavate trichogyne (arrow); (e) gonimoblast filaments with carposporangia (arrows); (f–i) *Paludicola periploca*: (f) well-developed whorls with loose carposporophytes (arrows); (g) developing carposporophyte with a knot of gonimoblast filaments; (h) mature carpogonium with clavate trichogyne (arrow); (i) carposporophyte with carposporangia (arrows); (j, m) *Paludicola phangiae*: (j) well-developed and compressed whorls with loose carposporophytes (arrows); (k) whorl with loose carposporophyte (arrow); (l) mature carpogonium with clavate trichogyne (arrow); (m) gonimoblast filaments with carposporangia (arrows). Scale bars: (j) = 250 µm; (f) = 200 µm; (a, k) = 100 µm; (b, g) = 50 µm; (c, i, m) = 25 µm; (d, e, h, l) = 10 µm (Fig. (l) reproduced with permission by Taylor & Francis from Johnston et al. (2014))

**Basionym:** *Batrachospermum vagum* (Roth) C. Agardh var. *periplocum* Skuja, Österr Bot Z 116: 62 (1969).

**Type:** diagnosis, page 62, figures 1–15, page 59 in Skuja (1969) (Lectotype, designated by Necchi 1990).

**Type locality:** Brazil, Amazonas, Negro River, north of Manaus, 02.197856° S, 61.136071° W.

**Description:** plants monoecious; branching pseudodichotomous; whorls well developed, contiguous, obconical or compressed and indistinct, 400–1300 µm in diameter; primary fascicles straight, with 8–15(–17) cells; secondary fascicles abundant and covering the entire internode; spermatangia on secondary fascicles, rarely on primary fascicles, 5–9 µm in diameter; carpogonial branches straight, composed of 3–9(–11) cells, developing from the periaxial cells, rarely from proximal cells or cortical filaments, 18–60(–75) µm in length; carpogonia 35–60 µm in length, 7–12 µm in diameter; carposporophytes loose, 400–550 µm in diameter, 200–280 µm in height, immature or aborted in some populations; carposporangia obovoidal or ellipsoidal, 12–16 µm in length, 9–13 µm in diameter; monosporangia present in some populations, spherical or sub-spherical, on primary or secondary fascicles, 8–11 µm in length, 8–10.5 µm in diameter.

**Diagnostic characters:** this species is distinguishable from other species in the genus by the combination of well-developed whorls, straight primary fascicles, loose carposporophytes that are higher than whorls and small carposporangia ( $\leq 16$  µm in length,  $\leq 13$  µm in diameter).

**Representative sequences in GenBank:** MN943944, MN943945 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.49).

**Key references:** Skuja (1969), Necchi (1990), Vis et al. (2020b).

*Paludicola phangiae* (ET Johnston, P-E Lim, and ML Vis) ML Vis and Necchi, J Phycol 56:858 (2020b) (Fig. 5.54j–m)

**Basionym:** *Batrachospermum phangii* ET Johnston, P-E Lim, and ML Vis, Phycologia 53:335 (2014).

**Type:** MICH1229175, ET Johnston, SP Ong, LY Chou and F Saint Amour, 01. ix.2011 (Holotype); BHO A-0979, KEP 216686, KLU 12149 (Isotypes).

**Type locality:** Malaysia, North Selangor, tributary of Sungai Endau, drainage ditch outside peat swamp alongside road, 3.655133° N, 101.319733° E.

**Description:** plants monoecious; branching irregular; whorls well developed, contiguous, compressed and indistinct, 600–800 µm in diameter; primary fascicles straight, 8–10 cells; secondary fascicles abundant, covering the entire internode; spermatangia on primary and secondary fascicles, 5–6 µm in diameter; carpogonial branches straight, composed of 3–7 cells, developing from pericentral cells, 15–35 µm in length; carpogonia 32–38 µm in length, 5–7 µm in diameter; carposporophytes loose, lower or as high as whorls, 225–357 µm in diameter and 220–300 µm in height; carposporangia obovoidal, 11–15 µm in length, 9–12 µm in diameter.

**Diagnostic characters:** this species can be differentiated from all others in the genus by the combination of straight primary fascicles, loose carposporophytes that are lower or the same height of whorls and small carposporangia ( $\leq 15 \mu\text{m}$  in length).

**Representative sequences in GenBank:** KF557564 (*rbcL*).

**Distribution:** Asia: Malaysia (Fig. 5.49).

**Key references:** Johnston et al. (2014), Vis et al. (2020b).

*Paludicola tapirensis* (Kumano and Phang) ML Vis and Necchi, J Phycol 56:858 (2020b) (Fig. 5.55a–d)

**Basionym:** *Batrachospermum tapirense* Kumano and Phang, Jap J Phycol 35: 259 (1987).

**Type:** KLU, SM Phang no. 216, 30.ix.1985 (Holotype).

**Type locality:** Malaysia, Johor, Sungai Tapir, tributary of Sungai Endau, 02.547927° N, 103.414326° E.

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical, 90–200  $\mu\text{m}$  in diameter; primary fascicles straight, with 4–6 cells; secondary fascicles abundant and covering the entire internode; spermatangia on primary or secondary fascicles, 4–6  $\mu\text{m}$  in diameter; carpogonial branches straight or slightly curved, composed of 4–6 cells, developing from the periaxial cells, 15–30  $\mu\text{m}$  in length; carpogonia with curved trichogynes, 30–40  $\mu\text{m}$  in length, 5–9  $\mu\text{m}$  in diameter; carposporophytes loose, indistinguishable and as high as whorls, 70–100  $\mu\text{m}$  in diameter and 30–60  $\mu\text{m}$  in height; carposporangia obovoidal or sub-spherical, 8–12  $\mu\text{m}$  in length and 5–8  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species can be differentiated from all others in the genus by the combination of straight primary fascicles, curved trichogynes, loose carposporophytes that are indistinguishable and same height of whorls and small carposporangia ( $\leq 12 \mu\text{m}$  in length,  $\leq 8 \mu\text{m}$  in diameter).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia (Fig. 5.49).

**Key references:** Kumano and Phang (1987), Kumano (2002), Vis et al. (2020b).

*Paludicola turfosa* (Bory) ML Vis and Necchi, J Phycol 56:854 (2020b) (Fig. 5.55e–h)

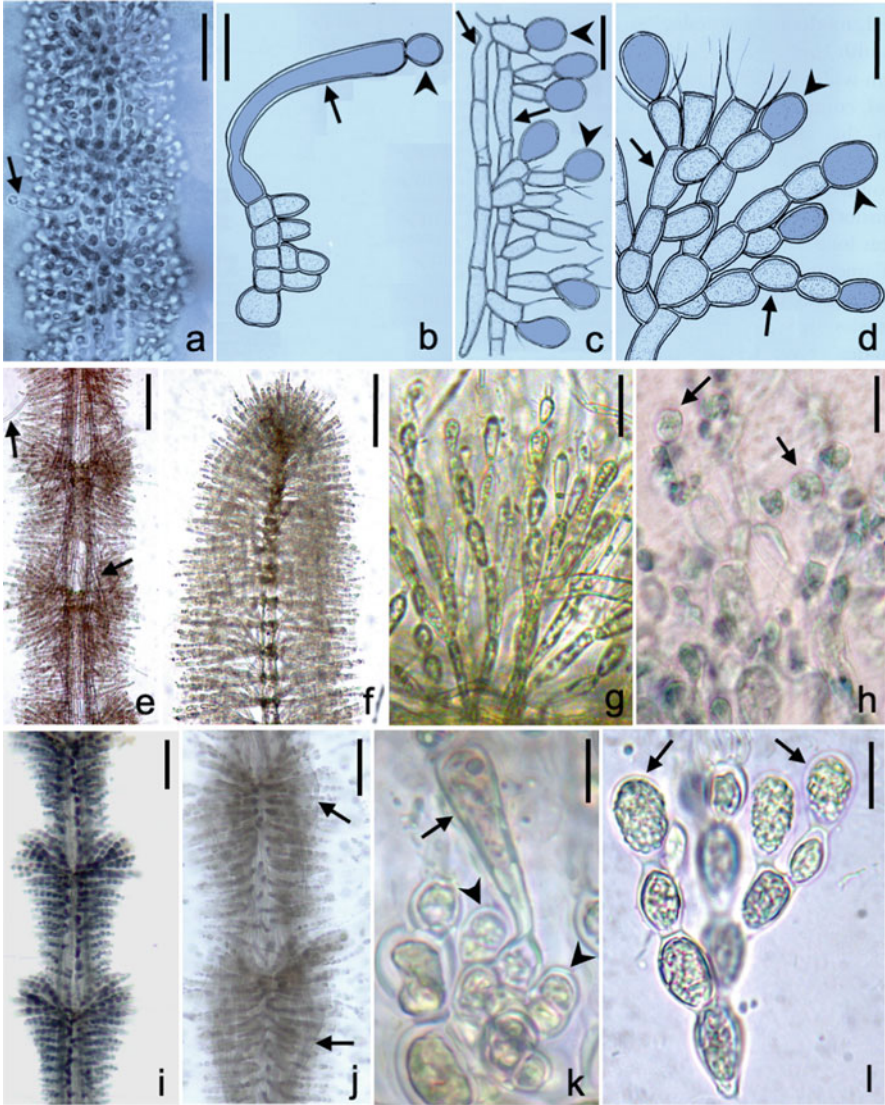
**Basionym:** *Batrachospermum turfosum* Bory, Ann Mus Hist Nat 12:32 (1808b).

**Type:** PC0591558, Herbarium Thuret, M Thore, vi.180X (Lectotype, designated by Compère 1991).

**Type locality:** France, Dax, 43.707007° N, 1.052702° W (estimated).

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical, barrel-shaped or compressed and indistinct, 235–375  $\mu\text{m}$  in diameter; primary fascicles straight, with (3–)5–8 cells; secondary fascicles abundant and covering the entire internode; spermatangia on primary or secondary fascicles, 7–10  $\mu\text{m}$  in diameter.





**Fig. 5.55** (a–d) *Paludicola tapirensis*: (a) reduced compressed whorls with an extruding trichogyne (arrow); (b) fertilized carpogonium with clavate and bent trichogyne (arrow) and attached spermatium (arrowhead); (c) prostrate gonimoblast filaments (arrows) with carposporangia (arrowheads); (d) erect gonimoblast filaments (arrows) with carposporangia (arrowheads); (e–h) *Paludicola turfosa*: (e) reduced obconical whorls with loosely arranged cortical filaments (arrows); (f) Apex with young whorls; (g) primary fascicle with cylindrical and ellipsoidal cells; (h) spermatangia (arrows) on fascicle cells; (i–l) *Paludicola turfosa*: (i) reduced obconical whorls; (j) obconical whorls with loosely arranged cortical filaments (arrows); (k) mature carpogonium with clavate trichogyne (arrow) and involucre filaments (arrowheads); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (e, i) = 100  $\mu\text{m}$ ; (f) = 50  $\mu\text{m}$ ; (g) = 25  $\mu\text{m}$ ; (b–d, h, j–l) = 10  $\mu\text{m}$  (Fig. (a–d) redrawn Kumano and Phang (1987))

**Diagnostic characters:** this species is morphologically similar to *P. groenbladii* and specimens with reduced whorls of *P. keratophyta*, both occurring primarily in Europe, the latter overlapping in distribution; they can be unequivocally distinguished based only on DNA sequence data.

**Representative sequences in GenBank:** MN943985 (COI-5P), MN943940, MN943942 (*rbcL*).

**Distribution:** Europe: Austria, Finland, France, Lithuania, Ireland, Poland, Scotland; North America: the USA (Fig. 5.49).

**Key references:** Sheath et al. (1994c), Eloranta et al. (2011), Vis et al. (2020b).

*Paludicola turfosisiformis* Necchi and ML Vis, J Phycol 56:856 (2020b) (Fig. 5.55i–l)

**Type:** SJRP 32590, LHZ Branco, 20.viii.2011 (Holotype).

**Type locality:** Brazil: Goiás, Alto Paraíso de Goiás, Chapada dos Veadeiros National Park, Salto Stream, 14.26444444° S, 47.6325° W.

**Description:** plants monoecious; branching pseudodichotomous; whorls reduced, contiguous, obconical, pear-shaped or compressed and indistinct, 160–500 µm in diameter; primary fascicles straight, with 3–7(–8) cells; secondary fascicles abundant and covering the entire internode; spermatangia on secondary fascicles, rarely on primary fascicles, 6–9 µm in diameter; carpogonial branches straight, composed of 3–7 cells, developing from the periaxial cells, rarely from proximal cells or cortical filaments, 17–30 µm in length; carpogonia 37–47 µm in length, 6.5–10 µm in diameter; carposporophytes dense, higher than whorls, 100–250 µm in diameter, 55–130 µm in height; carposporangia obovoidal, sub-spherical, or spherical, 10–13 µm in length, 8–12 µm in diameter.

**Diagnostic characters:** this species can be differentiated from all others in the genus by the combination of reduced whorls, straight primary fascicles, spermatangia on secondary fascicles, dense carposporophytes that are higher than whorls and small carposporangia ( $\leq 13$  µm in length,  $\leq 12$  µm in diameter).

**Representative sequences in GenBank:** MN943992, MN943993 (COI-5P), MN943948, MN943949 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.49).

**Key references:** Necchi (1990), Vis et al. (2020b).

## Genus *Sheathia*

*Sheathia* Salomaki and ML Vis, J Phycol 50:535 (2014)

**Heterotypic synonym:** *Batrachospermum* section *Helminthoidea* Sirodot ex De Toni, Syll Alg 4(1):55 (1897b).

**Type species:** *Sheathia boryana* (Sirodot) Salomaki and ML Vis, J Phycol 50: 535 (2014).



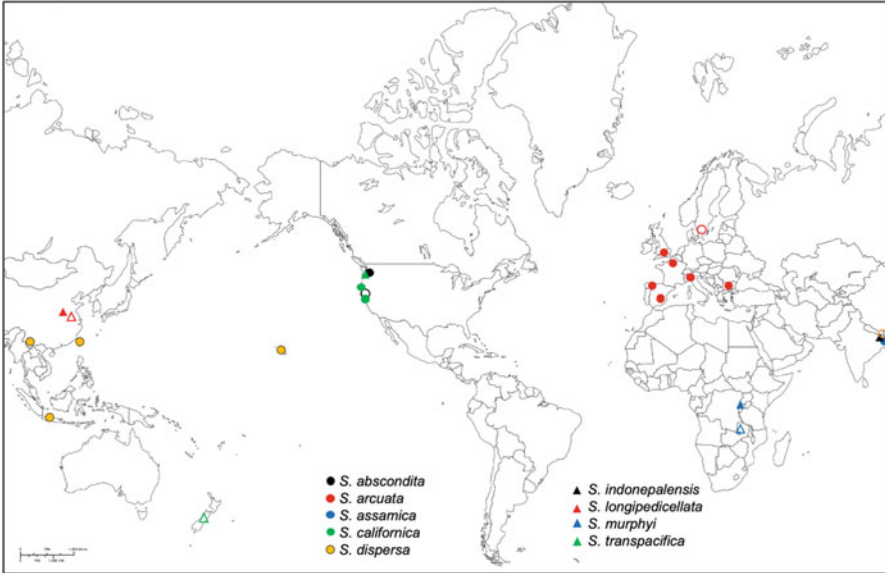
**Description:** thalli dioecious or monoecious; olive-drab to dark blue-green, purple to reddish; consistency mucilaginous, branching irregular; whorls well developed, often >1 mm in diameter, contiguous or separate, spherical or barrel-shaped; main axis covered by either heterocortication composed of both bulbous and cylindrical cells or homocortication composed of only cylindrical cells; primary fascicles with cells ranging from cylindrical to ellipsoidal and obovoidal or pear-shaped; secondary fascicles few and sparse or abundant and covering the entire internode in few species; spermatangia typically on primary or secondary fascicles, but can be at the tips of involucrel filaments of the carpogonial branches; carpogonial branches (24.1–)45.0–87.6(–129.3)  $\mu\text{m}$  in length, composed of cells similar to the fascicles, straight, developing from the periaxial, proximal cells of primary fascicles and occasionally from distal cells of primary fascicles; involucrel filaments, short or long, composed of cylindrical or ellipsoidal cells; carpogonia with sessile, rarely shortly stalked, cylindrical, sub-cylindrical, club-shaped, lanceolate or ellipsoidal trichogynes; carposporophytes pedunculate, spherical, inserted within the whorls or exerted, small; gonimoblast filaments densely arranged, composed of 2–4(–5) barrel-shaped to cylindrical cells; carposporangia small or large, spherical to obovoidal.

**Diagnostic characters:** this genus has the same characteristics as *Batrachospermum*, but seven species can be distinguished from *Batrachospermum* based on heterocortication. However, there are 10 species that do not have this character and can only be distinguished from *Batrachospermum* based on DNA sequence data.

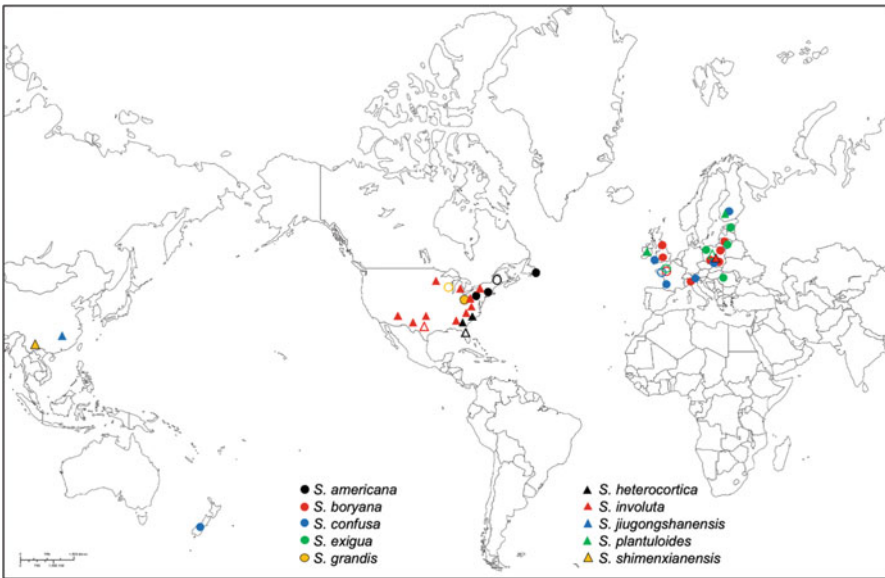
**Habitat:** This genus appears to have a wide ecological distribution as species can be collected in streams of temperate and tropical regions of the world. Some species have been frequently reported from alkaline streams and springs in North America, China, and Europe. Specimens belonging to this genus have often been collected as “Chantransia” without gametophytes in locations from Africa, China, the Hawaiian Islands, Indonesia, and Europe. In North America, specimens attributable to this genus have been collected from streams with wide ranging environmental data including mean current velocity 11–97  $\text{cm s}^{-1}$ , 3–24  $^{\circ}\text{C}$  water temperature, 5.5–8.5 pH, 20–890  $\mu\text{S cm}^{-1}$ . In Europe, *Sheathia* species (*S. arcuata*, *S. boryana*, *S. confusa* and *S. exigua*) have been collected from streams and springs with moderate temperature (14–16  $^{\circ}\text{C}$ ) and mildly alkaline to alkaline waters (pH 6.7–8.0, 120–715  $\mu\text{S cm}^{-1}$ ). In Asia, *Sheathia longipedicellata* has been reported from moderate temperature (11.5–15  $^{\circ}\text{C}$ ) and mildly alkaline (pH 6.5–7.2) waters.

**Distribution:** representatives of the genus have been reported in all continents, except South America—Africa: Rwanda, Zambia; Asia: Indonesia, India, Nepal, China, Taiwan; Australasia: New Zealand; Europe: Austria, Bulgaria, France, Finland, Lithuania, Ireland, Poland, Spain Sweden, the UK; North America: the USA, Canada; Pacific Islands: Hawaiian Islands (Figs. 5.56 and Fig. 5.57).

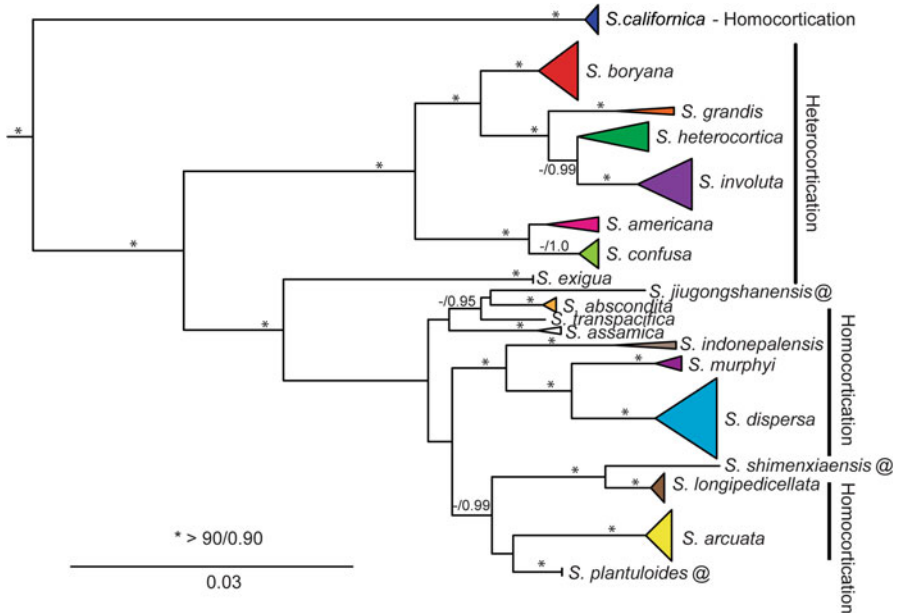
**Phylogenetic relationships among species:** analyses of the *rbcL* sequences show 14 clades and five single specimen branches within the genus (Fig. 5.58). Sister to



**Fig. 5.56** Map showing the distribution of *Sheathia* species with homocortication. Open symbols represent the type localities



**Fig. 5.57** Map showing the distribution of *Sheathia* species with heterocortication and those known only from chantransia. Open symbols represent the type localities



**Fig. 5.58** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Sheathia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities. Type of cortication is provided and species with @ are known from chantransia only

all of the species is the homocorticate species, *S. californica*. There is a clade of six exclusively heterocorticate species (*S. americana*, *S. boryana*, *S. confusa*, *S. grandis*, *S. heterocortica*, and *S. involuta*). A species with heterocortication only near the base of the thallus, *S. exigua* is sister to the large clade of eleven species, all of which are known to be homocorticate (*S. abscondita*, *S. arcuata*, *S. assamica*, *S. dispersa*, *S. indonepalensis*, *S. longipedicellata*, *S. murphyi*, and *S. transpacificca*); *S. jiugongshanensis*, *S. plantuloides*, and *S. shimexiaensis* are in the same clade but are known only from “Chantransia” stage such that this gametophyte character cannot be verified. There are no currently recognized species without sequence data and the total number of species within the genus is 19 (seven heterocorticate, nine homocorticate, and three known only from “Chantransia”).

**Key to the species of the genus *Sheathia*:** no key is presented for this genus. The species can be divided into those with homocortication and those with heterocortication. Among the homocorticate species, there are no morphological characteristics that do not significantly overlap to distinguish among species, but there are some geographic range differences. Among the heterocorticate species, only *S. confusa* has a unique morphological character and *S. exigua* only has heterocortication on the lower part of the plant; geographic ranges may differ among species.

### ***Species with homocortication (cylindrical cells only)***

Cannot be distinguished morphologically from each other and some members of the genus *Batrachospermum* and in most cases DNA sequence data are needed for positive identification although geography may be used to identify in some cases.

***Sheathia abscondita*** Stancheva, Sheath, and ML Vis, *Algae* 35:217 (2020a) (Fig. 5.59a–c)

**Type:** UC2085028, R Fadness, 15.vii.2015, (Holotype); BHO A-1653 (Isotype).

**Type locality:** the USA, California, South Fork Garcia River above Garcia River, 38.8553° N, 123.56022° W.

**Description:** thalli dioecious; whorls well developed, barrel-shaped or spherical, contiguous, 178–920 µm diameter; main axis covered in regular, cylindrical cortication; primary fascicles 17–23 cells; secondary fascicles sparse; carpogonial branches 2–8 cells; carpogonia 25–44 µm in length with clavate to lanceolate trichogynes 6.7–9.1 µm diameter; carposporophytes 1–5(–6) per whorl, 62–151 µm in diameter; carposporangia obovoidal, 10.2–14.0 µm in length, 7.2–9.2 µm diameter.

**Representative sequences in GenBank:** MT441852 (COI-5P); MT441833 (*rbcL*).

**Distribution:** North America: the USA; Pacific Islands: Hawaii (Fig. 5.56).

**Key reference:** Vis et al. (2020b).

**Remarks:** This species geographic range, overlaps with *S. californica*, *S. dispersa*, and *S. transpacificica*.

***Sheathia arcuata*** (Kylin) Salomaki and ML Vis, *J Phycol* 50:535 (2014) (Fig. 5.59d–f)

**Basionym:** *Batrachospermum arcuatum*, Kylin (1912: 22, fig. 7, a–e).

**Type:** S, Wittrock and Norstedt, *Algae exsiccatae* No. 1356b pro parte (Syntype).

**Type locality:** Sweden: Hör (current spelling Höör), Skåne, 55.934857° N, 13.539592° E (estimated).

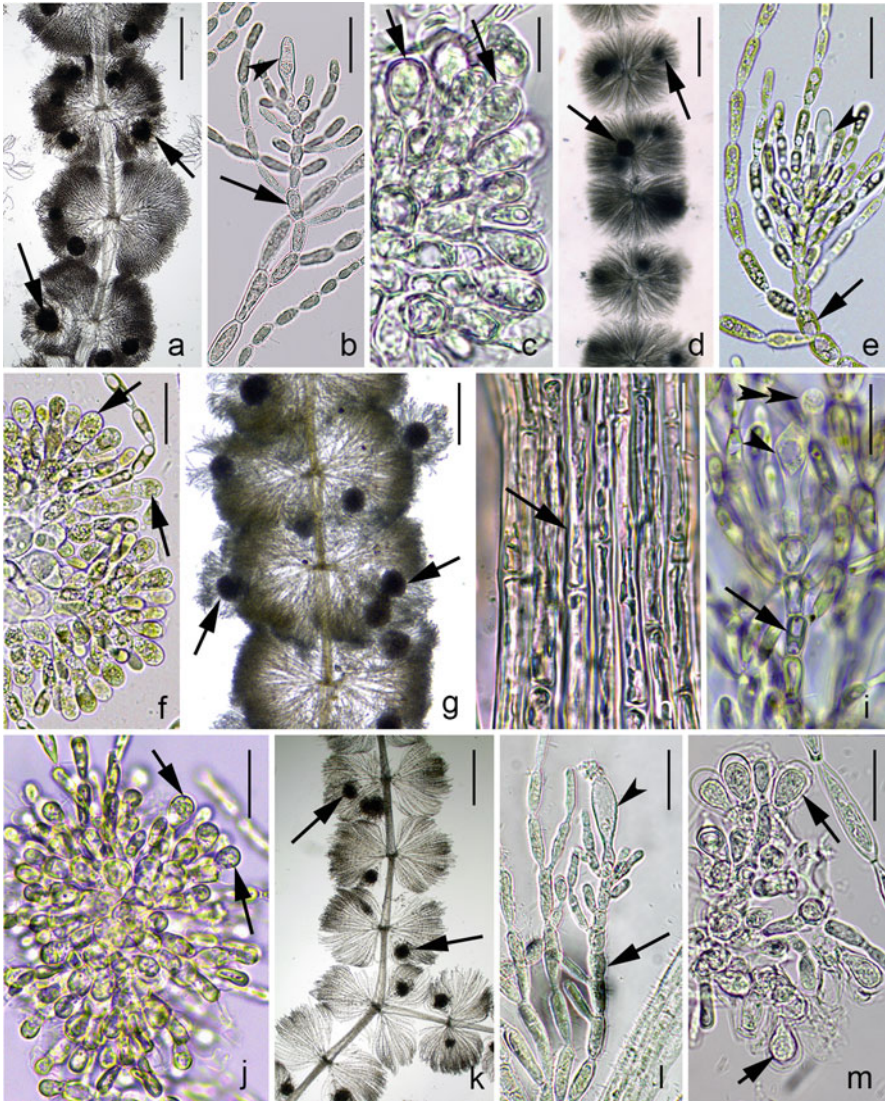
**Description:** thalli dioecious; whorls barrel-shaped or spherical, separate or contiguous, (358–)401–782(–1043) µm in diameter; main axis covered in regular, cylindrical cortication; primary fascicles 8–17 cells; secondary fascicles few and sparse; carpogonial branches 5–10(–16) cells; carpogonia (18.7–)22–39 µm in length with clavate trichogynes 6–12 µm diameter; carposporophytes 1–3(–6) per whorl, 75–204 µm diameter; carposporangia (9–)10–15(–19) µm in length and (6–)7–11(–12) µm diameter.

**Representative sequences in GenBank:** KM592945, KM592947 (COI-5P); JX669741, KM593804, KM077037 (*rbcL*).

**Distribution:** Europe: Bulgaria, France, Italy, Spain, Sweden, the UK (Fig. 5.56).

**Key references:** Vis et al. (1995, 2010, 2020b), Salomaki et al. (2014), Abdelahad et al. (2015).





**Fig. 5.59** (a–c) *Sheathia abscondita*: (a) spherical whorls with spherical, pedunculate carposporophyte (arrows); (b) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with ellipsoidal trichogyne (arrowhead); (c) carposporophyte with obovoidal carposporangia (arrows); (d–f) *Sheathia arcuata*: (d) barrel-shaped whorls with spherical, pedunculate carposporophyte (arrows); (e) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with ellipsoidal trichogyne (arrowhead); (f) carposporophyte with obovoidal carposporangia (arrows); (g–j) *Sheathia assamica*: (g) barrel-shaped whorls with spherical, pedunculate carposporophyte (arrows); (h) homocortication of the main axis composed of cylindrical cells (arrow); (i) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and attached spermatium (double arrowhead); (j) carposporophyte; (k–m) *Sheathia californica*: (k) spherical whorls with spherical, pedunculate carposporophyte (arrows); (l) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead); (m) carposporophyte with obovoidal carposporangia (arrows). Scale bars: (a, g, k) = 250 µm; (b, e, f) = 25 µm; (c) = 10 µm; (d) = 350 µm; (h, i) = 15 µm; (j, l, m) = 20 µm (Image author: Fig. (a, b, k) R Stancheva)



**Remarks:** Data from the type specimen in Vis et al. (1995) and specimens with DNA sequence data (Vis et al. 2010, Abdelahad et al. 2015) were utilized for the description. This species' geographic range overlaps *S. exigua* with heterocortication only on the lower portion of the thallus and some *Batrachospermum* species for which there are many morphological similarities.

*Sheathia assamica* Necchi, JA West, EK Ganesan, and F Yasmin, *Algae* 34:281 (2019b) (Fig. 5.59g–j)

**Type:** SJRP 32576, O Necchi Jr, F Yasmin, JA West, and EK Ganesan, 24.ii.2018 (Holotype).

**Type locality:** India; Assam, Morigaon District, Amsoi, 26.122111° N, 92.440250° E.

**Description:** thalli dioecious; whorls spherical and separate (male), barrel-shaped and contiguous (female), 374–870 µm in diameter; main axis covered in regular, cylindrical cortication; primary fascicles 11–16 cell; secondary fascicles lacking; spermatangia spherical, terminal on primary fascicles, 5.5–9.2 µm in diameter; carpogonial branches 3–9 cells; carpogonia 20.5–30.5 µm in length, with club-shaped or ellipsoidal trichogynes, 7–10 µm in diameter; carposporophytes 1–3 per whorl, 98.0–220.2 µm in diameter; carposporangia obovoidal, 10.8–17.9 µm in length, 7.5–11.7 µm diameter.

**Representative sequences in GenBank:** MN481450, MN481451 (*rbcL*).

**Distribution:** Asia: India (Fig. 5.56).

**Key reference:** Necchi et al. (2019b).

**Remarks:** this species' geographic range overlaps with *S. indonepalensis*.

*Sheathia californica* Stancheva, Sheath, and ML Vis, *Algae* 35:220 (2020a) (Fig. 5.59k–m)

**Type:** UC2085029, R Fadness, 16.vii.2016 (Holotype).

**Type locality:** the USA, California, Signal Creek at Big Cheese Road, Garcia River Watershed, 38.8748° N, 123.4937° W.

**Description:** thalli monoecious or dioecious; whorls well developed, barrel-shaped or spherical, contiguous, 320–890 µm diameter; main axis covered in regular, cylindrical cortication; primary fascicles (9–)12–18(–20) cells; secondary fascicles few and sparse; carpogonial branches 2–13 cells; carpogonia 21–42 µm in length with clavate to ellipsoidal trichogynes, 5.6–10.3 µm diameter; carposporophytes 1–4 per whorl, 68–142 µm in diameter; carposporangia obovoidal, 10.6–15.0(–16.3) µm in length, (7.5–)8.0–10.5(–13.1) µm diameter.

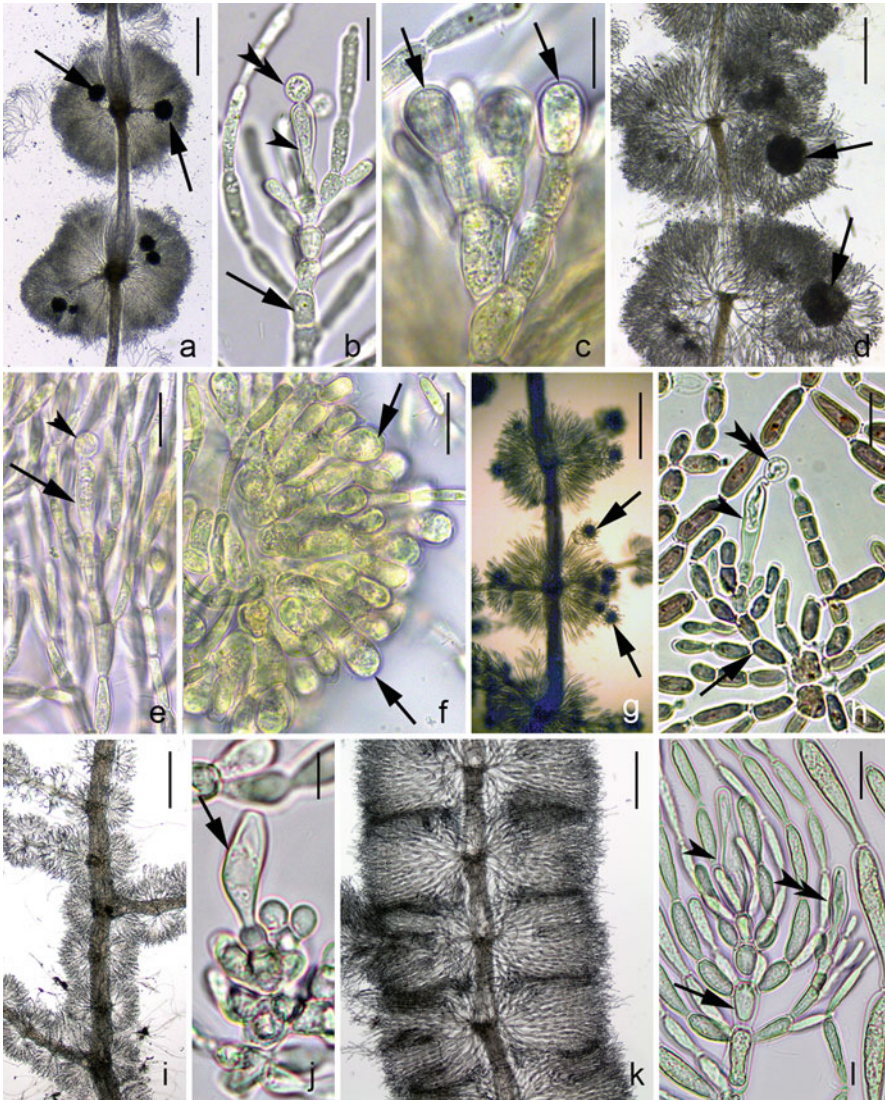
**Representative sequences in GenBank:** MT441854 (COI-5P); MT441834 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.56).

**Key reference:** Vis et al. (2020b).

**Remarks:** this species' geographic range overlaps with *S. abscondita*.

*Sheathia dispersa* Necchi, JA West, EK Ganesan, and SK Rai, *Algae* 34:286 (2019b) (Fig. 5.60a–c)



**Fig. 5.60** (a–c) *Sheathia dispersa*: (a) spherical whorls with spherical, pedunculate carposporophytes (arrows); (b) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and attached spermatium (double arrowhead); (c) carposporophyte with obovoidal carposporangia (arrows); (d–f) *Sheathia indonepalensis*: (d) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (e) carpogonium with ellipsoidal trichogyne (arrow) and attached spermatium (arrowhead); (f) carposporophyte with obovoidal carposporangia (arrows); (g, h) *Sheathia longipedicellata*: (g) spherical whorls with spherical, pedunculate carposporophytes (arrows); (h) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and attached spermatium (double arrowhead); (i–j) *Sheathia murphyi*: (i) spherical whorls; (j) carpogonium with clavate trichogyne (arrow); (k, l) *Sheathia transpacifica*: (k) contiguous, barrel-shaped whorls; (l) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and developing carpogonium (double arrowhead) on an involucre filament. Scale bars: (a, g) = 500  $\mu$ m; (b, e, f, h, j) = 15  $\mu$ m; (c, l) = 10  $\mu$ m; (d) = 200  $\mu$ m; (i, k) = 250  $\mu$ m (Figs. (g, h) reprinted with permission by Taylor and Francis from Vis et al. (2010))

**Type:** SJRP 32578, O Necchi Jr et al., 21.ii.2018 (Holotype).

**Type locality:** Nepal; Province no. 1, Koshi Zone, Morang District, Sundarharaicha Municipality, ward no. 5, Khayer Khola, 26.690222° N, 87.321694° E.

**Description:** thalli dioecious; whorls barrel-shaped or spherical, contiguous or separate, 483–1,316 µm diameter; main axis covered in regular, cylindrical cortication; primary fascicles 11–18 cells; secondary fascicles lacking; spermatangia spherical or obovoidal, terminal on primary fascicles, 5.8–8.1 µm in diameter; carpogonial branches 3–8 cells; carpogonia 20.6–29.6 µm in length, with club-shaped trichogynes, 5.8–7 µm in diameter; carposporophytes, 1–5 per whorl, 97–235 µm in diameter; carposporangia obovoidal, pear-shaped, or sub-spherical, 13–20 µm in length, 7.8–12.2 µm diameter.

**Representative sequences in GenBank:** KC596299, KC596316, JX669681 (COI-5P); DQ141320, EF116873, MN487058 (*rbcL*).

**Distribution:** Asia: China, Indonesia, Nepal, and Taiwan; Pacific Islands: Hawaii (Fig. 5.56).

**Key references:** Chou and Wang (2006), Vis et al. (2010), Necchi et al. (2019b).

**Remarks:** for some locations only *Chantransia* has been observed and these reports are based on DNA sequence data. Numerous publications refer to *Batrachospermum arcuatum* or *Sheathia arcuata*, but these specimens should be placed in this species based on DNA sequence similarity (see Vis et al. 2020a). A recent paper on *Chantransia* from China provided *rbcL* data for unnamed specimens that are within this species (Han et al. 2020).

*Sheathia indonepalensis* Necchi, JA West, EK Ganesan, SK Rai, and F Yasmin, *Algae* 34:284 (2019a) (Fig. 5.60d–f)

**Type:** SJRP 32575, O Necchi Jr, F Yasmin, JA West, and EK Ganesan, 23 February 2018 (Holotype).

**Type locality:** India, Assam, Nagaon District, Chapanalla, 26.320472° N, 92.902028° E.

**Description:** thalli dioecious; whorls barrel-shaped or spherical, contiguous or separate, 543–1,465 µm diameter; main axis covered in regular, cylindrical cortication; primary fascicles 12–23 cells; secondary fascicles lacking; spermatangia spherical or obovoidal, terminal on primary fascicles, 5.5–9.5 µm in diameter; carpogonial branches 4–9 cells; carpogonia 20.7–32 µm in length, with club-shaped trichogynes 6–8.5 µm diameter; carposporophytes 1–5 per whorl, 112–209 µm in diameter; carposporangia obovoidal, 11.4–17.2 µm in length, 8.2–11.4 µm diameter.

**Representative sequences in GenBank:** MN481449, MN487060 (*rbcL*).

**Distribution:** Asia: India, Nepal (Fig. 5.56).

**Key reference:** Necchi et al. (2019b).

**Remarks:** this species' geographic range overlaps with *S. assamica*.

*Sheathia longipedicellata* (D Hua and ZX Shi) JF Han, FR Nan, J Feng, JP Lv, Q Liu, Kociolek, and SL Xie, *Phytotaxa* 367:68 (2018) (Fig. 5.60g, h)

**Basionym:** *Batrachospermum longipedicellatum* D Hua and ZX Shi, *Acta Phytotax Sin* 34:324 (1996).

**Type:** XZTC 9102, no collector, no date.

**Type locality:** China: Jiangsu province, Xuzhou, 34.205768° N, 117.284124° E (estimated).

**Description:** thalli monoecious or dioecious; whorls spherical or barrel-shaped, separate, (167–)345–1,000 µm in diameter; main axis covered in regular, cylindrical cortication; primary fascicles (9–)10–14 cells; secondary fascicles lacking; spermatangia spherical, terminal, or lateral on fascicles, 5–9 µm in diameter; carpogonial branches (3–)5–8(–12) cells long; carpogonia 20–52 µm in length, trichogyne clavate, fusiform, long fusiform, 4–8 µm in diameter; carposporophytes 1–3(–6) per whorl, 62–167 µm in diameter; carposporangia obovoidal, (8.5–)10–15 µm in length, 5–9 µm diameter.

**Representative sequences in GenBank:** KC511071, KC511072 (COI-5P); GU457346, JQ028696, MH356749 (*rbcL*).

**Distribution:** Asia: China (Fig. 5.56).

**Key references:** Han et al. (2018, 2019), Hua and Shi (1996), Vis et al. (2010, 2020b), Xie and Feng (2007).

**Remarks:** The species description provided was compiled from descriptions of species considered synonymous [*S. hongdongensis*, *S. jinchengensis*, and *S. matouensis*; see Vis et al. (2020b)] and includes information from the key references. The only exception is the carpogonia dimensions for *S. matouensis* because the text states one size but the figures another. Its geographic range does not overlap the other homocorticate *Sheathia* species but overlaps *Batrachospermum shanxiense*.

*Sheathia murphyi* AL Szinte, JC Taylor, and ML Vis, *Phycologia* 59:194 (2020) (Fig. 5.60i, j)

**Type:** SANDC 19–565, JC Taylor, 02.vii.2011 (Holotype); BHO A-0947 (Isotype).

**Type locality:** Zambia; Northern Zambia, Luwumbu River, 10.746047° S, 33.442119° E.

**Description:** thalli potentially dioecious (no spermatangia observed); whorls well developed, barrel-shaped, separate, 260–339 µm in diameter; main axis covered in regular, cylindrical cortication; primary fascicles 4–8 cells; secondary fascicles few and sparse; carpogonial branches 4–5 cells; carpogonium 23–32 µm in length with trichogyne symmetrical or slightly asymmetrical, fusiform to clavate, 6–9 µm diameter; carposporophytes not observed.

**Representative sequences in GenBank:** MN974522 (COI-5P); MN974517, MT109264 (*rbcL*).

**Distribution:** Africa: Rwanda, Zambia (Fig. 5.56).

**Key references:** Fischer et al. (2020), Szinte et al. (2020).

**Remarks:** sequence data from *chantransia* specimens collected in Rwanda place them with this species (<0.4% sequence difference) and extend its geography range.

*Sheathia transpacific* ML Vis, *Algae* 35:221 (2020a) (Fig. 5.60k, l)

**Type:** NSW1060885, TJ Entwisle, 24.xi.2000, (Holotype); Isotypes NSW1060887, BHO A-1664.

**Type locality:** New Zealand, Wairarapa Stream Burnside, 43.508585° S, 172.584051° E.

**Description:** thalli dioecious; whorls well developed, barrel-shaped or spherical, contiguous, 513–810 µm diameter; main axis covered in regular, cylindrical cortication; primary fascicles 11–15 cells; secondary fascicles few and sparse; carpogonial branches 3–8 cells; carpogonia (28–)34–50(–68) µm in length with clavate, long-clavate, and ellipsoidal/fusiform trichogynes, 5.0–9.5 µm diameter; carposporophytes not observed.

**Representative sequences in GenBank:** MT441857 (COI-5P); MT441833 (*rbcL*).

**Distribution:** Australasia: New Zealand; North America: the USA (Fig. 5.56).

**Key reference:** Vis et al. (2020b).

### *Species with heterocortication (bulbous and cylindrical cells)*

These species cannot be distinguished morphologically from each other and in most cases DNA sequence data are needed for positive identification although geography may be used to identify in some cases.

*Sheathia americana* Salomaki and ML Vis, *J Phycol* 50:538 (2014) (Fig. 5.61a–d)

**Type:** NY 01840458, ML Vis, 16.vi.1997 (Holotype); BHO A-1110, MICH1229188 (Isotypes).

**Type locality:** the USA; Maine, Hancock County, East Hancock, Tunk Mountain, 44.64472° N, 68.10472° W.

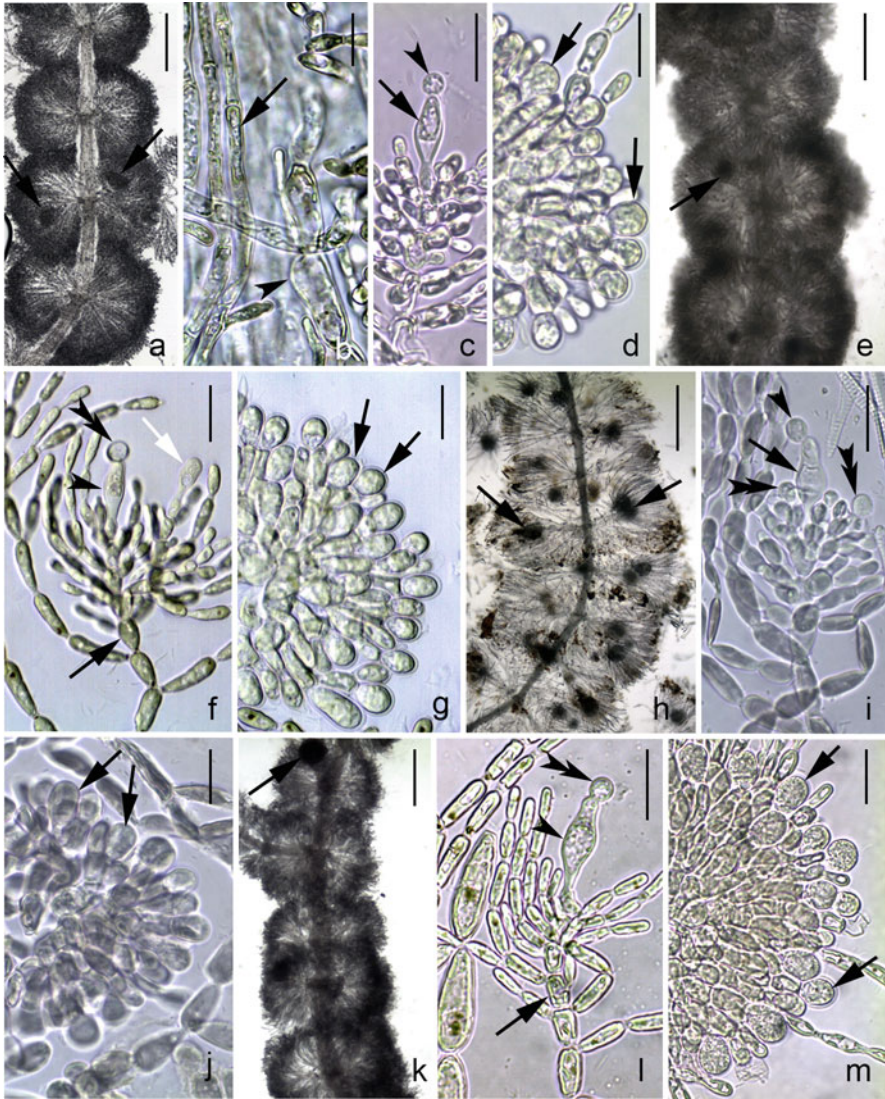
**Description:** thalli dioecious; whorls spherical, barrel-shaped, contiguous, 175 µm–>2 mm diameter; main axis, especially lower part of plant covered in heterocortication; primary fascicles 6–23 cells; secondary fascicles few and sparse; spermatangia terminal and sub-terminal on primary and secondary fascicles; carpogonial branches 4–15 cells; carpogonia 17–44 µm in length with clavate trichogynes, 5.5–10 µm diameter; carposporophytes one to many per whorl, 40–220 µm diameter; carposporangia spherical to obovoidal, 7–15 µm in length and 5–10 µm diameter.

**Representative sequences in GenBank:** JX669693, JX669697, JX669729 (COI-5P); JX669736, JX669756, JX669759 (*rbcL*).

**Distribution:** North America: Canada, the USA (Fig. 5.57).

**Key reference:** Salomaki et al. (2014).





**Fig. 5.61** (a–d) *Sheathia americana*: (a) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (b) heterocortication of the main axis with cylindrical cells (arrow) and bulbous cells (arrowhead); (c) carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) carposporophyte with spherical carposporangia (arrows); (e–g) *Sheathia boryana*: (e) barrel-shaped whorls with spherical, pedunculate carposporophyte (arrow); (f) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and attached spermatium (double arrowhead) as well as a developing carpogonium on an involucreal filament (white arrow); (g) carposporophyte with obovoidal carposporangia (arrows); (h–j) *Sheathia confusa*: (h) whorl; (i) carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead) as well as spermatangia on the involucreal filaments (double arrowhead); (j) carposporophyte with spherical carposporangia (arrows); (k–m) *Sheathia exigua*: (k) barrel-shaped whorls with spherical, pedunculate carposporophyte (arrow); (l) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with clavate trichogyne (arrowhead) and attached spermatium (double arrowhead); (m) carposporophyte with obovoidal carposporangia (arrows). Scale bars: (a, e, h) = 300 µm; (b–d, f, g, i, j, l, m) = 15 µm; (k) = 250 µm (Image author: Fig. (a–m) E Salomaki)

**Remarks:** this cryptic species was recently described. Previously, researchers had classified populations of this species as *Batrachospermum boryanum* (*S. boryana*). Based on DNA sequence data, *S. boryana* is only known from Europe.

*Sheathia boryana* (Sirodot) Salomaki and ML Vis, J Phycol 50:535 (2014)  
(Fig. 5.61e–g)

**Basionym:** *Batrachospermum boryanum* Sirodot (1874: 1366).

**Type:** PC0591464, S Sirodot, 12.v.1877 (Lectotype).

**Type locality:** France, Caniveau de la Trotinais, near Bourg-des-Comptes, south of Rennes, 47.929149° N, 1.741057° W (estimated).

**Description:** thalli monoecious or dioecious; whorls spherical, barrel-shaped, separate or contiguous, 286–1190 µm diameter; main axis covered in heterocortication; primary fascicles 7–18 cells; secondary fascicles abundant covering the entire internode; spermatangia terminal on fascicles; carpogonial branches 4–12(–20) cells; carpogonia 17–43 µm in length with short-clavate, clavate trichogynes 4.5–10 µm diameter; carposporophytes 1–30 per whorl, 55–197 µm diameter; carposporangia 7–17 µm in length and 6–14 µm diameter.

**Representative sequences in GenBank:** JX669707, JX669710 (COI-5P); KM593809, KM593823, KM593828 (*rbcL*).

**Distribution:** Europe: France, Lithuania, Poland, Italy, the UK (Fig. 5.57).

**Key references:** Salomaki et al. (2014), Abdelahad et al. (2015).

**Remarks:** Prior to Salomaki et al. (2014), this species (as *Batrachospermum boryanum*) was reported commonly from North America, but the records have been reassigned to *S. americana*, *S. grandis*, *S. heterocortica*, and *S. involuta*. To date, all DNA sequence data have shown *S. boryana* to be restricted to Europe.

*Sheathia confusa* (Bory) Salomaki and ML Vis, J Phycol 50:536 (2014)  
(Fig. 5.61h–j)

**Basionym:** *Batrachospermum ludibundum* var. *confusum* Bory, Ann Mus d'Hist Nat 12: 320 (1808b).

**Synonym:** *Batrachospermum confusum* (Bory) Hassall, A History of the British Freshwater Algae: 105 (1845).

**Type:** PC0591436, Bory, 1798, (Holotype).

**Type locality:** France, Brittany, near Fougerès, 48.351561° N, 1.204626° W (estimated).

**Description:** thalli monoecious; whorls barrel-shaped, contiguous, 164–1,510 µm diameter; main axis covered in heterocortication; primary fascicle 8–19 cells; secondary fascicles abundant covering entire internode; spermatangia terminal on fascicles and involucrel filaments of carpogonial branches; carpogonial branches 4–13 cells; carpogonia 14–38 µm in length with short-clavate, clavate trichogynes 5–11 µm diameter; carposporophytes 1–19 per whorl, 36–185 µm diameter; carposporangia (6.9–)8–15 µm in length and (4.7–)6–12 µm diameter.

**Diagnostic characters:** this species is recognized by spermatangia terminal on the involucrel filaments; however, the spermatangia may be difficult to find depending on time of year and maturity of specimen.

**Representative sequences in GenBank:** JX669711, JX669712, KM592954 (COI-5P); JX669781, KM593837, KM593846 (*rbcL*).

**Distribution:** Europe: Finland, France, Italy, Poland, Spain, the UK; Australasia: New Zealand (Fig. 5.57).

**Key references:** Vis et al. (1996b), Salomaki et al. (2014).

**Remarks:** Although Vis et al. (1996b) reported *S. confusa* (as *Batrachospermum confusum*) in North America, these records have not been substantiated with DNA sequence data and no specimens were reported in Salomaki et al. (2014).

*Sheathia exigua* Salomaki and ML Vis, J Phycol 50:536 (2014) (Fig. 5.61k–m)

**Type:** NY 01840460, WB Chiasson and ED Salomaki, 6.x.2011 (Holotype); BHO A-0905 MICH1229186 (Isotypes).

**Type locality:** France, near Corseul, adjacent to Chateau de Montafilan ruins, 48.487444° N, 2.190694° W.

**Description:** thalli dioecious; whorls contiguous, spherical to barrel-shaped, 301–1,236 µm diameter; heterocortication of the main axis in the lower part of the plant and cylindrical cortication on thinner axes; spermatangia terminal on fascicles; primary fascicle 8–16 cells; secondary fascicles few and sparse; carpogonial branches 5–13 cells; carpogonia 22–50 µm in length with clavate trichogynes 5.5–12.5 µm diameter; carpogonial branches 5–13 cells; carposporophytes one to many per whorl, sometimes exerted, 66–187 µm diameter; carposporangia obovoidal, 11–18 µm in length and 7–14 µm diameter.

**Diagnostic characters:** this species has heterocortication only on the lower part of the thallus and young thalli may not have this character. In Europe, it could be confused with the widespread species *S. boryana* with heterocortication and potentially *S. arcuata*, if heterocortication is not present.

**Representative sequences in GenBank:** JX669616 (COI-5P); JX669738 (*rbcL*).

**Distribution:** Europe: Bulgaria, Estonia, France, Lithuania, Poland (Fig. 5.57).

**Key reference:** Salomaki et al. (2014).

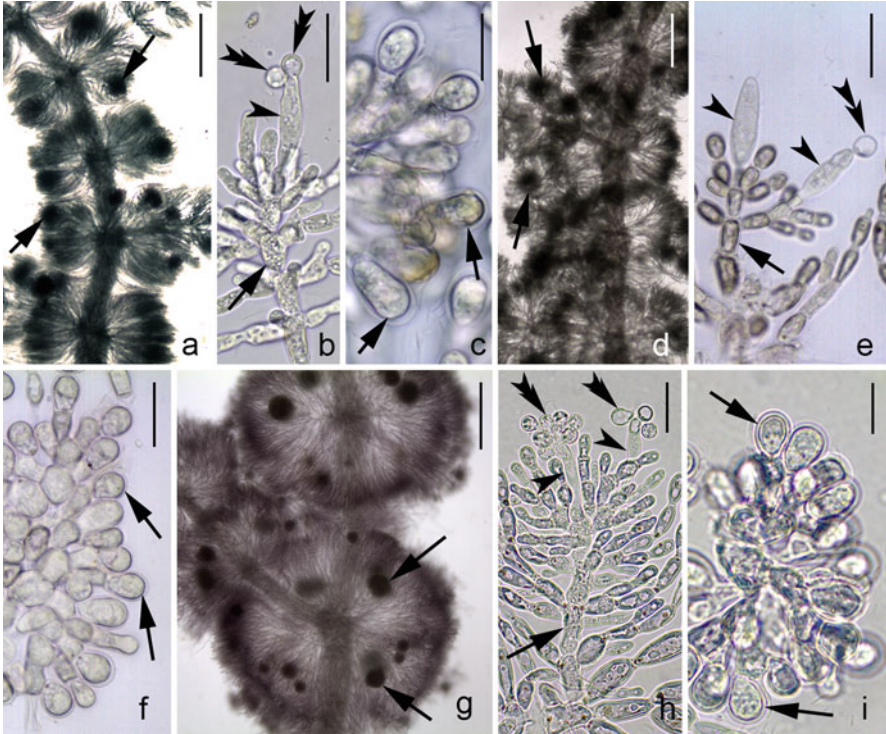
*Sheathia grandis* Salomaki and ML Vis, J Phycol 50:536 (2014) (Fig. 5.62a–c)

**Type:** NY 01840459, PA Schwartz, 6.x.2008 (Holotype); BHO A-0092, MICH1229187 (Isotypes).

**Type locality:** the USA, Wisconsin, Racine County, Tichigan Creek, 42.792222° N, 88.230278° W.

**Description:** thalli monoecious or dioecious; whorls spherical to barrel-shaped, 291–2,105 µm in diameter; main axis with heterocortication; primary fascicle 8–24 cells; secondary fascicles abundant covering the entire internode; spermatangia terminal on fascicles; carpogonial branches 5–17 cells; carpogonia (27.6–)32.0–58.2(–80.9) µm in length with clavate trichogynes, 6.1–12.8 µm diameter; carposporophytes one to many per whorl, sometimes exerted,





**Fig. 5.62** (a–c) *Sheathia grandis*: (a) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (b) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonium with ellipsoidal trichogyne (arrowhead) and attached spermatium (double arrowhead); (c) carposporophyte with obovoidal carposporangia (arrows); (d–f) *Sheathia heterocortica*: (d) barrel-shaped whorls with spherical, pedunculate carposporophytes (arrows); (e) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonia with ellipsoidal trichogynes (arrowheads) and attached spermatium (double arrowhead); (f) carposporophyte with obovoidal carposporangia (arrows); (g–i) *Sheathia involuta*: (g) spherical whorls with spherical, pedunculate carposporophytes (arrows); (h) carpogonial branch with cells undifferentiated from fascicle cells (arrow) and carpogonia with ellipsoidal trichogynes (arrowheads) and clusters of attached spermatia (double arrowheads); (i) carposporophyte with obovoidal carposporangia (arrows). Scale bars: (a, g) = 250 µm; (b, c, e, h, i) = 15 µm; (d) = 300 µm; (f) = 20 µm (Image author: Fig. (a–f) E Salomaki)

73–240 µm diameter; carposporangia obovoidal, (11.1–)13.2–21.0(–25.2) µm in length and (7.8–)9.3–13.9(–17.5) µm in diameter.

**Representative sequences in GenBank:** JX669699, JX669700 (COI-5P); JX669761, JX669762 (*rbcl*).

**Distribution:** North America: the USA (Fig. 5.57).

**Key reference:** Salomaki et al. (2014).

**Remarks:** this species may have been previously identified as *Batrachospermum boryanum* (*S. boryana*). Based on DNA sequence data, *S. boryana* is only known from Europe.

*Sheathia heterocortica* (Sheath and KM Cole) Salomaki and ML Vis, J Phycol 50: 536 (2014) (Fig. 5.62d–f)

**Basionym:** *Batrachospermum heterocorticum* Sheath and KM Cole, J Phycol 26: 566 (1990).

**Type:** UBC A70042, R Sheath, 05.v.1989, (Holotype).

**Type locality:** the USA, Florida, Marion County, Mormon Creek, 29.324722° N, 81.746667° W.

**Description:** thalli monoecious or dioecious; whorls separate or contiguous, spherical, 200–973 µm in diameter; main axis with heterocortication; primary fascicle 6–16 cells; secondary fascicles abundant covering the entire internode; spermatangia terminal and sub-terminal on fascicles; carpogonial branches 3–9 cells; carpogonia 20–50 µm in length with obconical, short stalked or sessile trichogynes 6–11 µm diameter; carposporophytes, many per whorl, 53–258 µm in diameter; carposporangia obovoidal, 9–16 µm in length and 6–11 µm diameter.

**Representative sequences in GenBank:** JX669718, JX669721, JX669735 (COI-5P); JX669765, JX669788, MG321564 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.57).

**Key references:** Sheath and Cole (1990), Salomaki et al. (2014).

*Sheathia involuta* (ML Vis and Sheath) Salomaki and ML Vis, J Phycol 50:536 (2014) (Fig. 5.62g–i)

**Basionym:** *Batrachospermum involutum* ML Vis and Sheath (1996:128, figs. 25–34).

**Type:** UBC A81614, RG Sheath & ML Vis, 01.xii.1993 (Holotype).

**Type locality:** the USA, Texas, San Marcos, 29.889487° N, 97.934197° W.

**Description:** thalli monoecious or dioecious; whorls separate or contiguous, spherical to barrel-shaped, 245–2,635 µm in diameter; main axis with heterocortication; primary fascicle 8–19 cells; secondary fascicles abundant covering the entire internode; spermatangia terminal on fascicles; carpogonial branches 6–19 cells; carpogonia 17.4–54 µm in length with clavate trichogynes 6.3–16.4 µm diameter; carposporophytes, one to many, sometimes exerted, 58–254 µm in diameter; carposporangia obovoidal, 9–18 µm in length and 7.8–17.5 µm diameter.

**Representative sequences in GenBank:** JX669705, JX669717, JX669730 (COI-5P); JX669747, JX669786, JX669800 (*rbcL*).

**Distribution:** North America: the USA; Europe: Poland (Fig. 5.57).

**Key references:** Vis and Sheath (1996), Salomaki et al. (2014).

### *Species Known from “Chantransia” Stage Only*

*Sheathia jiugongshanensis* JF Han, FR Nan, and SL Xie, Phytotaxa 441:51 (2020)

**Type:** SXU-HB17926, FR Nan, KP Fang & SL Shi, ix.2017 (Holotype).

**Type locality:** China, Hubei Province, Jiugong Mountain, 29.452932° N, 114.770533° E.



**Description:** “Chantransia” composed of reddish tufts of branched filaments; vegetative cells cylindrical, 42.2–55.6  $\mu\text{m}$  in length and 8.9–12.2  $\mu\text{m}$  diameter; monosporangia obovoidal or sub-spherical, 7.8–11.1  $\mu\text{m}$  in length and 5.6–7.8  $\mu\text{m}$  diameter.

**Diagnostic characters:** this species is only known from the “Chantransia” stage and gametophytes have yet to be identified for distinguishing morphological characters; currently, it can only be identified using sequence data.

**Representative sequences in GenBank:** MK746106 (*rbcL*).

**Distribution:** Asia: China (Fig. 5.57).

**Key reference:** Han et al. (2020).

*Sheathia plantuloides* ML Vis, *Algae* 35:220 (2020)

**Type:** BHO A-1658, J Lee, P Eloranta & W Kowalski, 16.v.2011, (Holotype); Isotype ZTS.

**Type locality:** Poland, River Bóbr, 51.256233° N, 15.520893° E.

**Description:** “Chantransia” composed of bluish green to red tufts of branched filaments; vegetative cells (21.6–)28.3–50.0(–61.0)  $\mu\text{m}$  in length and 7.8–14.5  $\mu\text{m}$  diameter; monosporangia obovoidal, (6.7–)8.0–11.1(–12.8)  $\mu\text{m}$  in length and (4.8–) 6.0–9.3  $\mu\text{m}$  diameter.

**Diagnostic characters:** this species is only known from the “Chantransia” stage and gametophytes have yet to be identified for distinguishing morphological characters; currently, it can only be identified using sequence data.

**Representative sequences in GenBank:** MT441856 (COI-5P); MT441849 (*rbcL*).

**Distribution:** Europe: Finland, Ireland, Poland (Fig. 5.57).

**Key reference:** Vis et al. (2020b).

*Sheathia shimexiaensis* JF Han, FR Nan, and SL Xie, *Phytotaxa* 441:51 (2020)

**Type:** SXU-YN19042, KP Fang, iv.2019 (Holotype).

**Type locality:** China, Yunnan Province, Yuxi City, Shimen Gorge, 23.968000° N, 101.519000° E.

**Description:** “Chantransia” composed of brownish tufts of branched filaments; vegetative cells cylindrical, 28.9–50.0  $\mu\text{m}$  in length and 7.8–11.1  $\mu\text{m}$  in diameter; monosporangia obovoidal or sub-spherical, 6.7–11.1  $\mu\text{m}$  in length, and 5.6–10.0  $\mu\text{m}$  diameter.

**Diagnostic characters:** this species is only known from the “Chantransia” stage and gametophytes have yet to be identified for distinguishing morphological characters; currently, it can only be identified using sequence data.

**Representative sequences in GenBank:** MN272375 (*rbcL*).

**Distribution:** Asia: China (Fig. 5.57).

**Key reference:** Han et al. (2020).

## ***Doubtful Species***

***Sheathia carpoinvolucra*** (Sheath and ML Vis) Salomaki and ML Vis, in Salomaki et al. *J Phycol* 50:536 (2014). This species is most likely an ecological variant of *S. involuta*. The type locality was sampled and no specimens with the distinguishing character were collected, but *S. involuta* was identified using DNA sequencing. As noted in the protologue, carpogonia on involucral filaments have been noted in other taxa, but not on the filaments immediately subtending the carpogonium, which seems to be a minor distinction.

***Sheathia fluitans*** (Kerner) Salomaki and ML Vis, *J Phycol* 50:536 (2014).

This species was recognized by Vis et al. (1995) as a distinct species based on long carpogonia. Although the carpogonium length (52–65  $\mu\text{m}$ ) is longer than most other species in the genus, it does overlap *S. grandis* from North America and slightly overlaps *S. involuta* which is primarily North American but does occur in part of Poland.

## **Genus *Sirodotia***

***Sirodotia*** Kylin, *Nova Acta Reg Soc Sci Upsal Ser 3*:38 (1912)

**Type species:** *Sirodotia suecica* Kylin, *Nova Acta Reg Soc Sci Upsal Ser 3*:38 (1912).

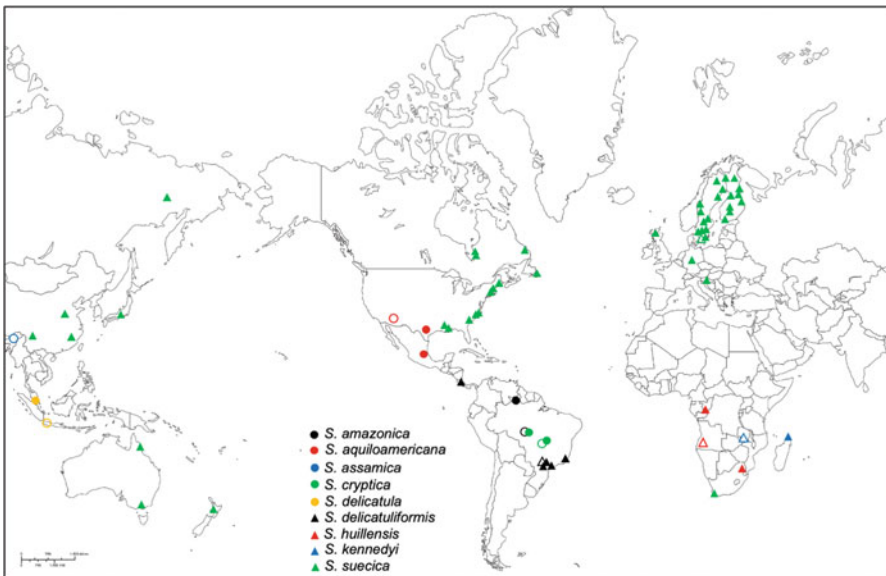
**Description:** plants monoecious, dioecious, or polyecious, greenish-blue to yellowish green, consistency mucilaginous; branching irregular; whorls well developed or reduced, contiguous or separate, obconical or pear-shaped; main axis covered by cylindrical cells; primary fascicles with cells variable in shape, cylindrical, ellipsoidal, obovoidal, sub-spherical, or spherical; secondary fascicles abundant, covering the entire or two-thirds of internode; spermatangia spherical, sub-spherical, or obovoidal on primary or secondary fascicles in groups of 1–3 or forming clusters; carpogonial branches well differentiated from the fascicles, straight, rarely curved, developing from the periaxial, proximal cells of primary fascicles or cortical filaments, less often from middle and distal cells of primary fascicles or rarely on the secondary fascicles, short, composed of disc- or barrel-shaped cells; involucral filaments few and short, composed 1–4 cylindrical or ellipsoidal cells; carpogonia asymmetrical, with a hemispherical protuberance in the basal portion; trichogynes sessile and cylindrical, elongate-cylindrical, elongate-conical, clavate, fusiform, lageniform, ellipsoidal, pear-shaped or irregularly shaped, with or without wavy margins; carposporophyte diffuse extending along the internode; gonimoblast filaments develop on the same side or opposite side of the basal protuberance of the carpogonium; gonimoblast filaments prostrate and indeterminate, composed of cylindrical cells, producing short, erect branches, formed by cylindrical or ellipsoidal cells, with terminal or sub-terminal

carposporangia; carposporangia large or small, obovoidal, ellipsoidal, or sub-spherical.

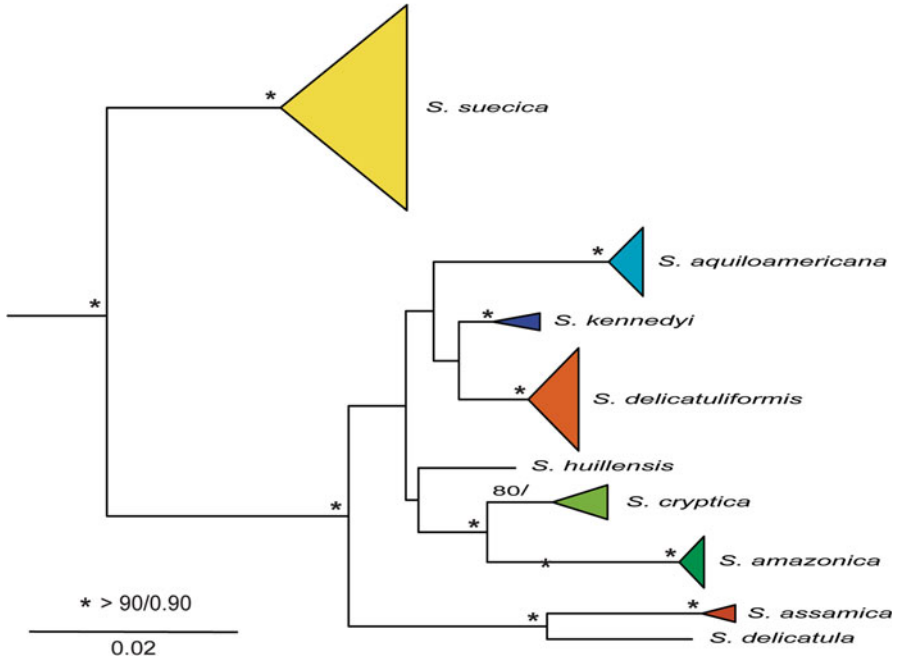
**Diagnostic characters:** the genus is characterized by diffuse carposporophytes composed of prostrate indeterminate gonimoblast filaments producing short, erect filaments with terminal carposporangia; and asymmetric carpogonium, with a semi-spherical basal protuberance; the shape of the whorls (obconical or pear-shaped with secondary fascicles covering the entire or half of the internode length) can be used as a secondary character; however, it is not exclusive to the genus and can be observed in species of *Kumanoa* (Necchi and Vis 2012), *Paludicola* (Vis et al. 2020b) and to varying degrees in other genera of Batrachospermales.

**Habitat:** in North America, the species of *Sirodotia* have been reported in the following conditions: temperature 8–18 °C, conductivity 10–140  $\mu\text{S cm}^{-1}$ , pH 5.7–7.6, and current velocity 19–106  $\text{cm s}^{-1}$  (Necchi et al. 1993); in South America, the species were collected in streams with temperature 10.5–24.5 °C, conductivity 8–110  $\mu\text{S cm}^{-1}$ , pH 6.5–7.3 and current velocity 17–65(–160)  $\text{cm s}^{-1}$  (Necchi 1991; Necchi et al. 1999); the only species known from Europe (*S. suecica*) has been reported in waters with temperature 10.2–25.8 °C (mean 18.2 °C), conductivity 18–381  $\mu\text{S cm}^{-1}$  (mean 48  $\mu\text{S cm}^{-1}$ ), and pH 5.6–7.4 (mean 6.3) (Eloranta et al. 2016).

**Distribution:** the genus has been collected in temperate, tropical, subtropical, and sub-polar regions of Africa, Asia, Australasia, Europe, North and South America (Fig. 5.63).



**Fig. 5.63** Map showing the distribution of *Sirodotia* species. Open symbols represent the type localities



**Fig. 5.64** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Sirodotia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

**Remarks:** in a recent revision of the genus, Rossignolo et al. (2021) provided rationale for *S. cirrhosa* Skuja ex MS Balakrishnan & BB Chaugule, *S. gardneri* Skuja ex L. Flint and *S. huangshanensis* ZX Shi and SL Xie being considered doubtful species and as such they are not included here.

**Phylogenetic relationships among species:** sequence data of the *rbcL* are available for all nine species currently recognized in *Sirodotia* (Fig. 5.64). The genus is monophyletic with high support; all species with more than one sequence form highly supported clades (except *S. cryptica* with high support only for posterior probability), and two species are positioned on long branches (*S. delicatula* and *S. huillensis*). *Sirodotia suecica* has moderate intraspecific genetic variation (2.4%) and is a clade distant from the other species which are in a large clade with high support. Only two infrageneric groups are well supported and appear to reflect geographic distribution: *S. cryptica* and *S. amazonica* from South America (Brazil); and *S. assamica* and *S. delicatula* from Asia (India, Indonesia, and Malaysia). The intraspecific genetic divergences were low in all species ( $\leq 0.7\%$ ), except in *S. cryptica* (2.2%); the genetic variation in *S. cryptica* and *S. suecica* may suggest cryptic diversity within the species.

Key to the species of the genus *Sirodotia*

1a	Whorls reduced, primary fascicles 3–6(–8) cells	2
1b	Whorls well developed, primary fascicles (5–)6–13 cells	3
2a	Erect gonimoblast filaments 1-celled, carposporangia $\leq 10$ $\mu\text{m}$ in length, $\leq 7$ $\mu\text{m}$ in diameter	<i>S. kennedyi</i>
2b	Erect gonimoblast filaments 1–4 cells, carposporangia $\geq 10$ $\mu\text{m}$ in length, $> 8$ $\mu\text{m}$ in diameter	<i>S. amazonica</i>
3a	Carposporangia small, $\leq 10$ $\mu\text{m}$ in length	<i>S. huillensis</i>
3b	Carposporangia large, $\geq 10$ $\mu\text{m}$ in length	4
4a	Spermatangia arranged in clusters	<i>S. assamica</i>
4b	Spermatangia single or in groups of 2–3	5
5a	Gonimoblast initial developing from the non-protuberant side of the carpogonium	<i>S. suecica</i>
5b	Gonimoblast initial developing from the protuberant side of the carpogonium	6
6a	Known distribution restricted to Asia (Indonesia, Japan, and Malaysia)	<i>S. delicatula</i>
6b	Known distribution in the Americas	7
7a	Carposporangia wide, (7–)8–11 $\mu\text{m}$ in diameter	<i>S. cryptica</i>
7b	Carposporangia narrow, 6–8.5(–9.5) $\mu\text{m}$ in diameter	8
8a	Known distribution in southern North America (Costa Rica) and South America (Brazil)	<i>S. delicatuliformis</i>
8b	Known distribution in arid regions of North America (USA, Mexico)	<i>S. aquiloamericana</i>

***Sirodotia amazonica*** Necchi, NL Rossignolo and MO Paiano, Cryptogam Algal 42: 101 (2021) (Fig. 5.65a–d)

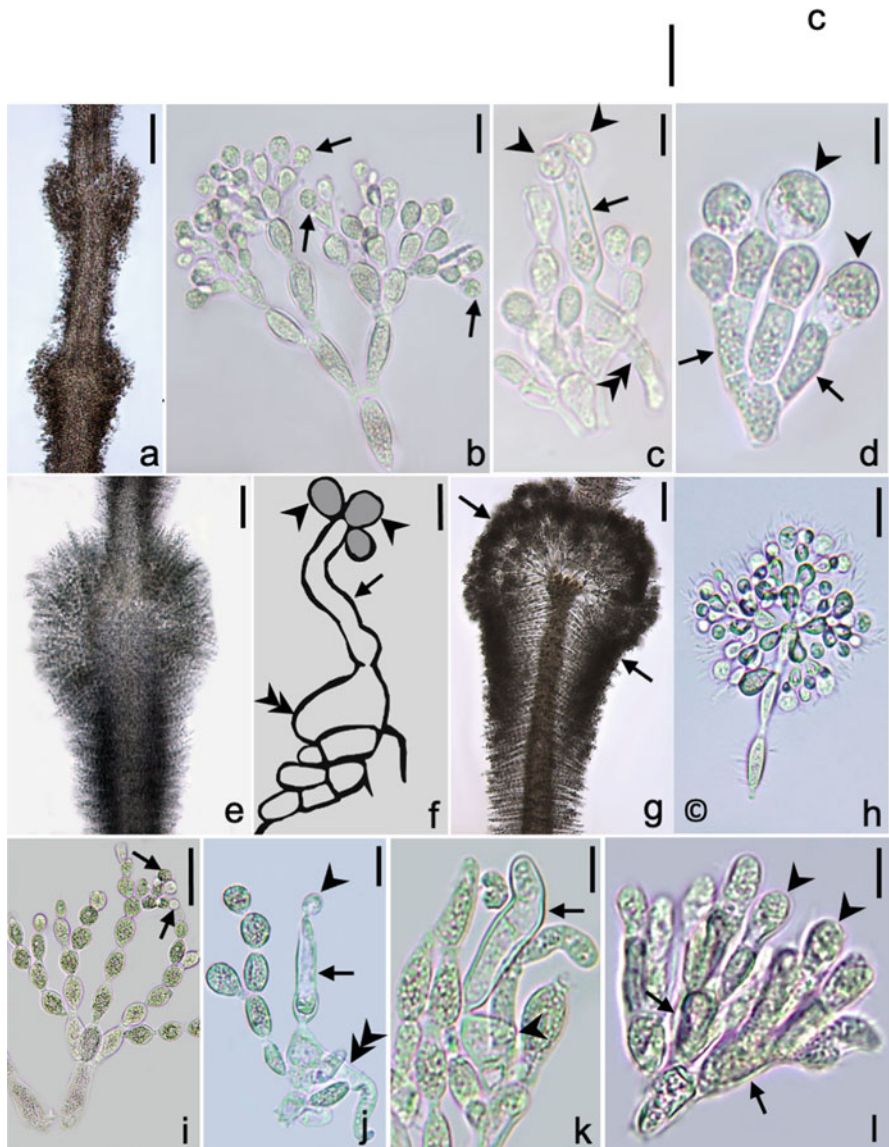
**Type:** SJRP 31924, O Necchi Jr., 27.ix.2010 (Holotype).

**Type locality:** Brazil, Mato Grosso, River Rosana, Route BR-163, between Sinop and Sorriso, 11.957222° S, 55.516944° W.

**Description:** plants monoecious or dioecious; whorls reduced, 249–491  $\mu\text{m}$  in diameter; primary fascicles 4–8 cells; spermatangia spherical or obovoidal, 6–9  $\mu\text{m}$  in diameter; carpogonial branches composed of 1–4 disc- or barrel-shaped cells, 8.5–25  $\mu\text{m}$  in length; carpogonia with sessile, elongate cylindrical usually with wave margins or fusiform trichogynes, 35–58(–62)  $\mu\text{m}$  in length, 8–14(–15)  $\mu\text{m}$  in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 1–4 cells; carposporangia obovoidal or sub-spherical, 10–18(–19)  $\mu\text{m}$  in length, (7–) 8–13  $\mu\text{m}$  in diameter.

**Diagnostic characters:** *Sirodotia amazonica* is very similar to two species also in Brazil, *S. delicatuliformis* and *S. cryptica*, overlapping for most morphological characters. However, *S. amazonica* is differentiated from *S. delicatuliformis* based on the wider carposporangia [8–13 versus 6–8.5(–9.5)  $\mu\text{m}$  in diameter] but cannot be distinguished from *S. cryptica* without DNA sequence data.





**Fig. 5.65** (a–d) *Sirodotia amazonica*: (a) obconical whorls; (b) primary fascicle with spermatangia (arrows); (c) fertilized carpogonium with trichogyne (arrow), attached spermatia (arrowheads), and gonimoblast initial developing from the protuberant side of the carpogonial base (double arrowhead); (d) erect gonimoblast filaments (arrows) and carposporangia (arrowheads); (e, f) *Sirodotia aquiloamericana*: (e) pear-shaped whorl; (f) fertilized carpogonium with trichogyne (arrow) and attached spermatia (arrowheads); (g, h) *Sirodotia assamica*: (g) obconical whorl with dense clusters of spermatangia (arrows); (h) primary fascicle with spermatangia arranged in clusters (arrow); (i–j) *Sirodotia cryptica*: (i) primary fascicle with spermatangia (arrows); (j) fertilized carpogonium with trichogyne (arrow), attached spermatium (arrowhead), and gonimoblast initial developing from the protuberant side of the carpogonial base (double arrowhead); (k, l) *Sirodotia delicatula*: (k) mature carpogonium with trichogyne (arrow) and protuberance in the carpogonial base (arrowhead); (l) erect gonimoblast filaments (arrows) and carposporangia (arrowheads). Scale bars: (a, e, g) = 100  $\mu\text{m}$ ; (i) = 50  $\mu\text{m}$ ; (h) = 25  $\mu\text{m}$ ; (b–d, j–l) = 10  $\mu\text{m}$ ; (f) = 5  $\mu\text{m}$  (All figures reproduced with permission by the Publications Scientifiques du Muséum National d’Histoire Naturelle, Paris, from Rossignolo et al. (2021))

**Representative sequences in GenBank:** KF010489, KF010490 (COI-5P), KC951866, KC951867 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.63).

**Key references:** Paiano and Necchi (2013), Rossignolo et al. (2021).

*Sirodotia aquiloamericana* Necchi, NL Rossignolo, and ML Vis, Cryptogam Algal 42:102 (2021) (Fig. 5.65e, f)

**Type:** BHO-0437, TA Dempster, 24.iv.2011 (Holotype).

**Type locality:** the USA, Arizona, outlet canal of Montezuma, 34.649167° N, 111.752222° W.

**Description:** Plants dioecious; whorls well developed, 408–675 µm in diameter; primary fascicles 7–12 cells; spermatangia spherical or obovoidal, 1–3, few or abundant on primary or secondary fascicles, 5–7(–8) µm in diameter; carpogonial branches composed of 1–3 disc- or barrel-shaped cells, 11–14 µm long; carpogonia with sessile, elongate cylindrical (with wavy margins) or fusiform trichogynes, 29–42 µm in length, 6–7.5 µm in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 2–5 cells; carposporangia obovoidal, 10–13 µm in length, 6–8 µm in diameter.

**Diagnostic characters:** this species most closely resembles *S. delicatuliformis* based on the narrow carposporangia, 6–8.5(–9.5) µm in diameter but differs in having wider whorls (408–675 versus 169–491 µm in diameter, respectively) and geographical distribution (arid regions of North America versus southern North America and South America, respectively). Previous records of this species were as *S. huillensis* (Necchi et al. 1993; Vis and Sheath 1999; Lam et al. 2012) from North America but *S. huillensis* is currently recognized as restricted to Africa.

**Representative sequences in GenBank:** EU636739 (COI-5P); JN408523, JF344716, AF126414 (*rbcL*).

**Distribution:** North America: Mexico, the USA (Fig. 5.63).

**Key references:** Necchi et al. (1993), Vis and Sheath (1999), Lam et al. (2012), Rossignolo et al. (2021).

*Sirodotia assamica* NL Rossignolo, F Yasmin, JA West, EK Ganesan, and Necchi O, Phytotaxa 437:121–134 (2020) (Fig. 5.65g, h)

**Type:** SJRP 32584. F Yasmin, 25.ii.2019 (Holotype).

**Type locality:** India, Assam, Nagaon District, Chapanalla, 26.320472° N, 92.17125° E.

**Description:** plants dioecious or monoecious; whorls well developed, 400–665 µm in diameter; primary fascicles, 6–11(–12) cells; spermatangia spherical, arranged in clusters on primary or secondary fascicles, 6–8 µm in diameter; carpogonial branches straight or slightly curved, 1–5(–6) disc- or barrel-shaped cells, 7–23 µm in length; carpogonia with sessile, elongate cylindrical, ellipsoidal, or lageniform trichogynes, 37–64 µm in length, 10–14(–16) µm in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments

with erect branches of 1–4 cells; carposporangia obovoidal, 11–14  $\mu\text{m}$  in length, 6–8  $\mu\text{m}$  in diameter.

**Diagnostic characters:** *Sirodotia assamica* can be distinguished by spermatangia arranged in dense clusters.

**Representative sequences in GenBank:** MN508239, MN508240 (COI-5P); MN496129, MN496130 (*rbcL*).

**Distribution:** Asia: India (Fig. 5.63).

**Key references:** Rossignolo et al. (2020, 2021).

*Sirodotia cryptica* Necchi, NL Rossignolo, and MO Paiano, Cryptogam Algal 42: 104 (2021) (Fig. 5.65i, j)

**Type:** SJRP 32575, FR Borges, 15.iv.2014 (Holotype).

**Type locality:** Brazil, Goiás, Highway GO-070, between the municipalities of Jussara and Itaberaí, 16.009083° S, 48.932194° W.

**Description:** plants monoecious or dioecious; whorls well developed, 223–559  $\mu\text{m}$  in diameter; primary fascicles (4–)5–10(–11) cells; spermatangia spherical or obovoidal, 6–9  $\mu\text{m}$  in diameter; carpogonial branches 1–4 disc- or barrel-shaped cells, 10–25  $\mu\text{m}$  in length; carpogonia with sessile, elongate cylindrical usually with wavy margins, elongate-conical or fusiform trichogynes, sometimes bent, (24–)26–58  $\mu\text{m}$  in length, 9–13(–15)  $\mu\text{m}$  in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 2–5 cells; carposporangia sub-spherical, ellipsoidal, or obovoidal, 10–17  $\mu\text{m}$  in length, (7–)8–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is very similar to two species also occurring in Brazil, *S. amazonica* and *S. delicatuliformis*. However, *S. cryptica* can be differentiated from *S. delicatuliformis* based on the wider carposporangia (8–13 and 6–8.5(–9.5)  $\mu\text{m}$  in diameter, respectively); this species and *S. amazonica* can only be distinguished with DNA sequence data.

**Representative sequences in GenBank:** KF010488, KF010491 (COI-5P); KC951865, KC951869 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.63).

**Key references:** Paiano and Necchi (2013), Rossignolo et al. (2021).

*Sirodotia delicatula* Skuja, Arch Hydrobiol Suppl 15:614 (1938) (Fig. 5.65k, l)

**Type:** UPS A-003747, Sunda German Limnological Expedition, 19.ix.1928 (Lectotype, designated by Rossignolo et al. 2021).

**Type locality:** Indonesia, Java Island, Bogor, Tijiwiwong, 6.589167° S, 106.805278° E.

**Description:** plants monoecious or dioecious; whorls well developed, 137–484  $\mu\text{m}$  in diameter; primary fascicles, 5–10 cells, proximal cells cylindrical or ellipsoidal, distal cells sub-spherical or obovoidal; spermatangia spherical or obovoidal, single or in pairs, (4–)7–8  $\mu\text{m}$  in diameter; carpogonial branches composed of 2–5 (–7) disc- or barrel-shaped cells, 8–17(–20)  $\mu\text{m}$  in length; carpogonia with sessile, elongate-cylindrical (with wavy margins), fusiform, ellipsoidal, or clavate trichogynes, (19–)24–70  $\mu\text{m}$  in length, 5–13  $\mu\text{m}$  in diameter; gonimoblast initial

developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 2–4 cells; carposporangia obovoidal, (8–)10–16  $\mu\text{m}$  in length, 5–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is morphologically similar to four species (*S. delicatuliformis*, *S. amazonica*, *S. cryptica*, and *S. aquiloamericana*) by having large carposporangia, spermatangia single or in pairs on primary fascicles and gonimoblast initial developing from the protuberant side of carpogonium. It is distinguishable from those species only by its geographic distribution (restricted to Asia versus Americas) and DNA sequence data.

**Representative sequences in GenBank:** KF557560 (*rbcL*).

**Distribution:** Asia: Indonesia, Malaysia (Fig. 5.63).

**Key references:** Skuja (1938), Johnston et al. (2014), Rossignolo et al. (2021).

*Sirodotia delicatuliformis* Necchi, NL Rossignolo, and MO Paiano, Cryptogam Algol 42:106 (2021) (Fig. 5.66a–c)

**Type:** SJRP 31918, O Necchi Jr, 25.vi.2008 (Holotype).

**Type locality:** Brazil, São Paulo State, Mirassol, São José dos Dourados River, 20.8125° S, 49.574722° W.

**Description:** plants monoecious, dioecious, or polyecious; whorls well developed, 169–491  $\mu\text{m}$  in diameter; primary fascicles 5–10(–13) cells; spermatangia spherical or obovoidal, single or in pairs, 5–8(–8.5)  $\mu\text{m}$  in diameter; carpogonial branches composed of 0–4 disc- or barrel-shaped cells, 6–22  $\mu\text{m}$  in length; carpogonia with sessile, elongate cylindrical (with wavy margins) or fusiform trichogynes, sometimes bifurcated or with bent end, (20–)22–55(–59)  $\mu\text{m}$  in length, 8–14(–16)  $\mu\text{m}$  in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 1–4 cells; carposporangia obovoidal or ellipsoidal, 11–16  $\mu\text{m}$  in length, 6–8.5(–9.5)  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to *S. amazonica*, *S. cryptica*, and *S. aquiloamericana* from North and South America; it is distinguished from *S. amazonica* and *S. cryptica* based on the narrow carposporangia (6–8.5(–9.5) versus 8–13  $\mu\text{m}$  in diameter), and from *S. aquiloamericana* by having smaller whorls (169–491 versus 408–675  $\mu\text{m}$  in diameter) and being restricted to South America.

**Representative sequences in GenBank:** KF010483, KF010486, KF010487 (COI-5P); KC951857, KC951858, KC951863 (*rbcL*).

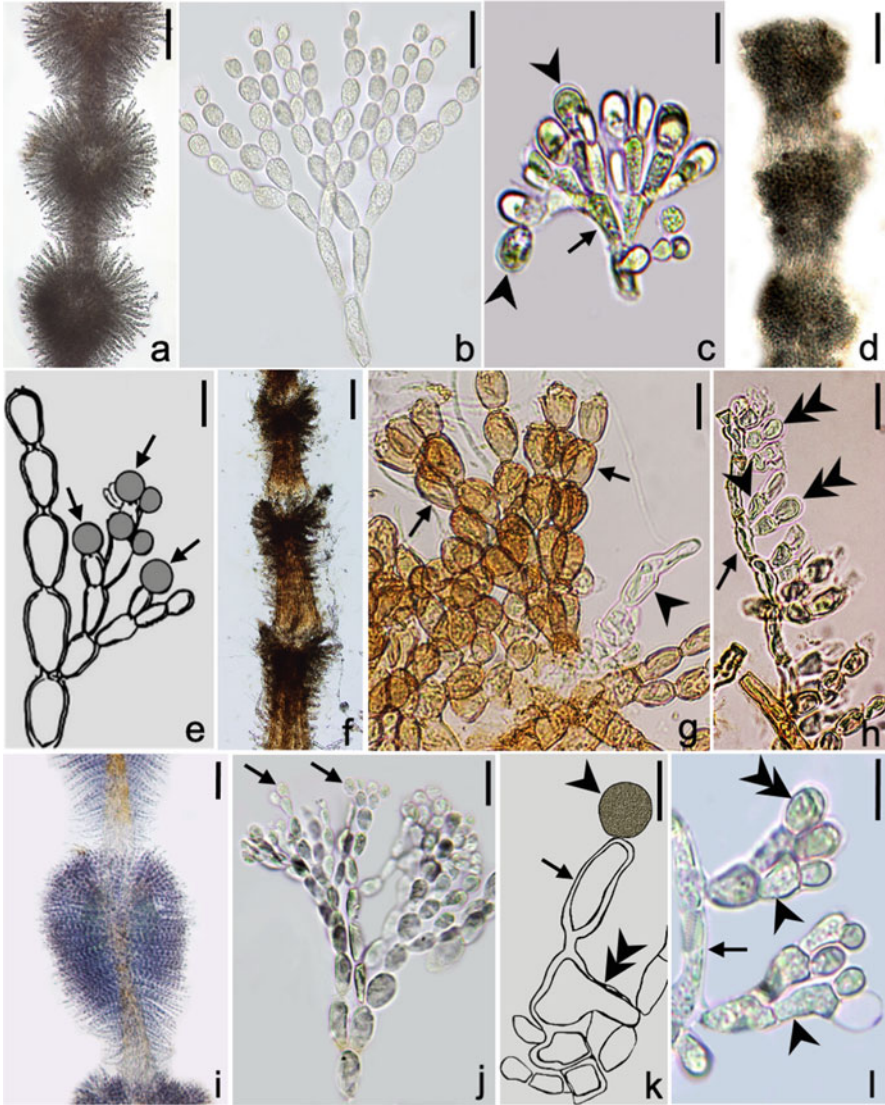
**Distribution:** North America: Costa Rica; South America: Brazil (Fig. 5.63).

**Key references:** Necchi (1991), Necchi et al. (2007), Paiano and Necchi (2013), Rossignolo et al. (2021).

*Sirodotia huillensis* (Welwitsch ex W West and GS West) Skuja, Arch Protistenk 74:304 (1931) (Fig. 5.66d, e)

**Basionym:** *Batrachospermum huillense* Welwitsch ex West and GS West, J Bot 35: 3 (1897).





**Fig. 5.66** (a–c) *Sirodotia delicatuliiformis*: (a) obconical whorls; (b) primary fascicle (arrows); (c) fertilized carpogonium with trichogyne (arrow), attached spermatia (arrowheads), and gonimoblast initial developing from the protuberant side of the carpogonial base (double arrowhead); (d, e) *Sirodotia huillensis*: (d) pear-shaped whorl; (e) tip of primary fascicle with spermatangia (arrows); (f–h) *Sirodotia kennedyi*: (f) obconical whorl; (g) primary fascicle (arrows) with mature carpogonium (arrowhead); (h) prostrate (arrow) and erect (arrowhead) gonimoblast filaments with carposporangia (double arrowheads); (i–l) *Sirodotia suecica*: (i) obconical whorl; (j) primary fascicle with spermatangia (arrows); (k) fertilized carpogonium with trichogyne (arrow), attached spermatium (arrowhead) and gonimoblast initial developing from the carpogonial base (double arrowhead); (l) prostrate (arrow) and erect (arrowhead) gonimoblast filaments with carposporangia (double arrowheads). Scale bars: (a, d, f, i) = 100  $\mu$ m; (b) = 50  $\mu$ m; (h, j, l) = 20  $\mu$ m; (c, e, g, k) = 10  $\mu$ m (All figures reproduced with permission by the Publications Scientifiques du Muséum National d’Histoire Naturelle, Paris, from Rossignolo et al. (2021))



**Type:** BM 001043858, FMJ Welwitsch, v.1860 (Holotype); LISU (Isotype).

**Type locality:** Africa, Angola, Huila, Lopollo, 14.7975° S, 14.6675° W.

**Description:** plants monoecious or dioecious; whorls well developed, 162–364 µm in diameter; primary fascicles (5–)6–10 cells, proximal cells cylindrical, ellipsoidal, or obovoidal, distal cells sub-spherical, obovoidal, or ellipsoidal; spermatangia, single or in pairs, spherical, 1–3, 5–7 µm in diameter; carpogonial branches composed of 1–3 disc- or barrel-shaped cells, 5–14 µm in length; carpogonia with sessile, elongate cylindrical with wavy margins, ellipsoidal, fusiform, or lageniform trichogynes, 28.5–48 µm in length, 5.5–12 µm in diameter; gonimoblast initial developing from the protuberant side of the carpogonium; gonimoblast filaments with erect branches of 2–4 cells; carposporangia obovoidal, 8–10 µm in length, 5–8 µm in diameter.

**Diagnostic characters:** this species is most similar to *S. kennedyi* based on the reduced whorls, short carposporangia and both occurring only in Africa; it differs from *S. kennedyi* in the number of cells in primary fascicle [5–9(–10) and 3–5, respectively], shorter carpogonial branches (1–3 and 3–4 cells, 5–14 and 16–22 µm in length, respectively), and a higher number of cells in the erect gonimoblast filament (2–4 and 1–2 cells, respectively).

**Representative sequences in GenBank:** MN974523 (COI-5P); JF344717 (*rbcL*).

**Distribution:** Africa: Angola, Democratic Republic of Congo, South Africa (Fig. 5.63).

**Key references:** Skuja (1931), Necchi et al. (1993), Lam et al. (2012), Rossignolo et al. (2021).

*Sirodotia kennedyi* AL Szinte, JC Taylor, and ML Vis, Phycologia 59:194 (2020) (Fig. 5.66f–h)

**Synonym:** *S. masoalensis* E Fischer, D Killmann and D Quandt, Pl. Fung. Syst. 65: 164 (2020).

**Type:** SANDC 19-566, MP Kennedy, 07.vii.2011 (Holotype); BHO A-0946 (Isotype).

**Type locality:** Zambia, Mutinondo River, Mutinondo Wilderness, 12.457704° S, 31.291006° E.

**Description:** plants dioecious; whorls reduced, 115–315 µm in diameter; primary fascicles, 3–5 cells; secondary fascicles present, covering half to the entire internode; spermatangia spherical, on primary or secondary fascicles, 6–8 µm in diameter; carpogonial branches composed of 3–4 disc- or barrel-shaped cells, arising from proximal cells of primary fascicles, short, 16–22 µm in length; carpogonia with sessile, elongate pear-shaped, elongate conical or irregularly shaped trichogynes, 25–40 µm in length, 7–11 µm in diameter; gonimoblast filaments with erect branches of one cell; carposporangia obovoidal or ellipsoidal, 9–10 µm in length, 5–7 µm in diameter.

**Diagnostic characters:** this species is most closely comparable to *S. huillensis* based on the reduced whorls, short carposporangia, and the occurrence in Africa only; it differs from *S. huillensis* in fewer cells of the primary fascicle (3–5 and

5–9(–10) cells, respectively), longer carpogonial branches (3–4 and 1–3 cells, 16–22 and 5–14  $\mu\text{m}$  in length, respectively) and having 1–2 cells in the erect gonimoblast filament.

**Representative sequences in GenBank:** MT109276 (COI-5P); MN974518, MT109266 (*rbcL*).

**Distribution:** Africa: Madagascar, Zambia (Fig. 5.63).

**Key references:** Fischer et al. (2020), Szinte et al. (2020), Rossignolo et al. (2021).

*Sirodotia suecica* Kylin, Nova Acta Regiae Soc Sci Ups 3:38 (1912) (Fig. 5.66i–l)

**Type:** LD, H Kylin, 3.viii.1909 (Lectotype); UPS A-653877 (Isolectotype).

**Type locality:** Sweden, Skåne, Osby, 56.383611° N, 13.992778° E.

**Description:** plants monoecious or dioecious; whorls well developed (135–) 200–850  $\mu\text{m}$  in diameter; primary fascicles, 4–12(–13) cells; spermatangia, single or in pairs, spherical or ellipsoidal, (4–)5–9  $\mu\text{m}$  in diameter; carpogonial branches composed of (1–)2–9 disc- or barrel-shaped cells, 5–40  $\mu\text{m}$  in length; carpogonia with sessile, elongate cylindrical, ellipsoidal, elongate pear-shaped or irregularly shaped trichogynes, (15–)19–48  $\mu\text{m}$  in length, (4–)5–16  $\mu\text{m}$  in diameter; gonimoblast initial developing from the non-protuberant side of the carpogonium; gonimoblast filaments with erect branches of 2–9 cells; carposporangia obovoidal, ellipsoidal, spherical, or pear-shaped, 10–21  $\mu\text{m}$  in length, 6–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar to *S. delicatula*, *S. delicatuliformis*, *S. amazonica*, *S. cryptica*, and *S. aquiloamericana* based on large carposporangia, but differentiated by the gonimoblast initial developing from the opposite side of the basal protuberance of carpogonium.

**Distribution:** Africa: South Africa; Asia: China, Japan; Australasia: Australia; Europe: Croatia, Finland, Germany, Russia, Sweden; North America: Canada, the USA (Fig. 5.63).

**Representative sequences in GenBank:** EU636737, MN974524 (COI-5P); JF344724, JF344725 (*rbcL*).

**Key references:** Necchi et al. (1993), Necchi et al. (2007), Lam et al. (2012), Rossignolo et al. (2021).

## Genus *Torularia*

*Torularia* Bonnemaison, Mém Mus Hist Nat 16:97 (1828)

**Synonyms:** *Batrachospermum* section *Setacea* De Toni, Sylloge Algar 4:57 (1897b); *Nothocladus* section *Setaceus* (De Toni) Entwisle and ML Vis, J Phycol 52:391 (2016); *Setacea* (De Toni) Necchi and NL Rossignolo, Phycologia 29:343 (2016); *Atrophycus* Necchi and NL Rossignolo, Notulae Algar 26:1 (2017).

**Type species:** *T. atra* (Hudson) MJ Wynne, Notulae Algar 89:2 (2019).

**Description:** thalli monoecious, dioecious, or polyecious, dark greenish-blue, brownish, or blackish, consistency mucilaginous; branching irregular; whorls

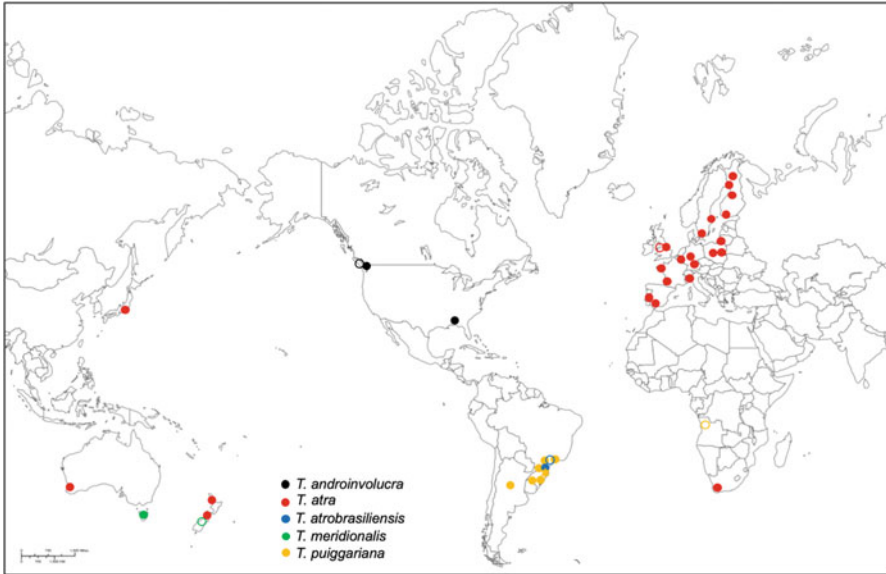
reduced, contiguous or separated, obconic, pear-shaped, or barrel-shaped; cortication of the main thallus axis well developed with filaments of cylindrical cells; primary fascicles formed by audouinelloid cells, ranging from cylindrical to barrel-shaped; secondary fascicles abundant and covering two-thirds to the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, straight or slightly curved, short, 1–5 cells, developing from the periaxial or proximal cells of primary fascicles, rarely on secondary fascicles or cortical filaments, composed of disc- or barrel-shaped cells; involucrel filaments, short, composed of short-cylindrical or barrel-shaped cells; carpogonia with unstalked, ellipsoidal, cylindrical, or clavate trichogynes; carposporophytes axial, hemispherical, or spherical, higher than whorls, 1–2 per whorl, large; gonimoblast filaments densely arranged, composed of cylindrical or barrel-shaped cells; carposporangia small, obovoidal, pear-shaped, or ellipsoidal.

**Diagnostic characters:** the genus is characterized by having reduced whorls, fascicles formed by audouinelloid cells, carpogonial branches well differentiated from the fascicles, straight or slightly curved and short; carposporophytes axial, centrally inserted and higher than the whorls; and gonimoblast filaments of one type, densely arranged and arising radially from the fertilized carpogonia. The most distinguishing character of this genus (reduced whorls) is also observed in the genus *Notohesperus* and in species of the genera *Kumanoa*, *Nothocladus*, *Paludicola*, and *Sirodotia*. But in combination with the other characters *Torularia* can be clearly distinguished from those genera.

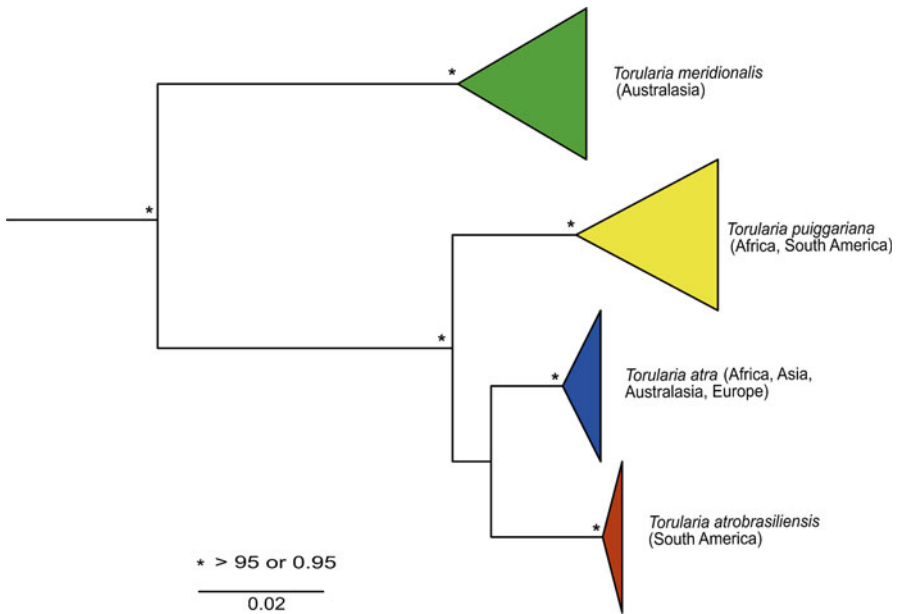
**Habitat:** species of *Torularia* occur predominantly in unpolluted waters, with relatively low temperatures (10.8–19.3 °C, rarely 22.5 °C), mildly acidic to circum-neutral pH (5.6–7.4, rarely 7.9), well oxygenated (61–92% saturation), and moderately to fast flowing (39–71 cm s<sup>-1</sup>, rarely 112 cm s<sup>-1</sup>), partly shaded or open streams and low specific conductances (3–153 μS cm<sup>-1</sup>, rarely up to 750 μS cm<sup>-1</sup>) (Eloranta et al. 2016; Rossignolo and Necchi 2016).

**Distribution:** representatives of the genus have been reported in temperate or sub-tropical, less often in tropical regions of Africa, Asia, Australasia, Europe, North and South America (Fig. 5.67).

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences within the genus based on data reported in the most recent study (Rossignolo and Necchi 2016) showed four clades with high support (Fig. 5.68), each one representing one species, as follows: *T. atra* (Africa, Asia, Australasia, and Europe), *T. atrobrasiliensis* (South America), *T. meridionalis* (Australasia) and *T. puiggariana* (Africa and South America). There is one species without sequence data (*T. androinvolucra*) that is distinguished by morphology and geographic distribution.



**Fig. 5.67** World map showing the distribution of the species of *Torularia*. Open symbols represent the type localities



**Fig. 5.68** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Torularia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

Key to the species of the genus *Torularia*

1a	Whorls compact, primary and secondary fascicles adherent to each other and to cortical cells	<i>T. puiggariana</i>
1b	Whorls not compact, primary and secondary fascicles not adherent	2
2a	Spermatangia only on involucrel filaments of carpogonial branches, distribution restricted to North America	<i>T. androinvolucra</i>
2b	Spermatangia on primary and secondary fascicles, never on involucrel filaments of carpogonial branches, not occurring in North America	3
3a	Distribution on more than one continent (Africa, Asia, Australasia, and Europe)	<i>T. atra</i>
3b	Distribution restricted to one continent (South America or Australasia)	4
4a	Distribution only in South America (Brazil)	<i>T. atrobrasilensis</i>
4b	Distribution only in Australasia (Australia)	<i>T. meridionalis</i>

***Torularia androinvolucra*** (Sheath, ML Vis, and KM Cole) Necchi and ML Vis, comb. nov. (Fig. 5.69a–d)

**Basionym:** *Batrachospermum androinvolucrum* Sheath, ML Vis, and KM Cole, J Phycol 29:722 (1993).

**Type:** UBC A80771, RG Sheath, 15.viii.1989 (Holotype).

**Type locality:** Canada, British Columbia, Vancouver Island, Route 4, 8 km NE from Ucluelet, Last Shoe Creek, 48.945897° N, 125.564766° W.

**Description:** thalli monoecious; whorls contiguous or separated, obconical or pear-shaped, 70–165 µm in diameter; primary fascicles not adherent to each other and to axial and cortical cells, curved, with 3–6 cells; secondary fascicles abundant and covering two-thirds to the entire internode; spermatangia 3–6 µm in diameter on involucrel filaments; carpogonial branches straight, composed of 1–3 disc- or barrel-shaped cells, developing from the periaxial of primary fascicles, 3–12 µm in length; involucrel filaments bearing spermatangia; carpogonia with sessile and clavate trichogynes, 14–32.5 µm in length, 3–6.5 µm in diameter; carposporophytes 1 per whorl, 125–145 µm in diameter and 35–105 µm in height; gonimoblast filaments with 3–5 barrel-shaped or short-cylindrical cells; carposporangia obovoidal or sub-spherical, 7–13 µm in length, 5.5–8.5 µm in diameter.

**Diagnostic characters:** this species is distinct from all others of the genus by the presence of spermatangia restricted to involucrel filaments.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** North America: Canada, the USA (Fig. 5.67).

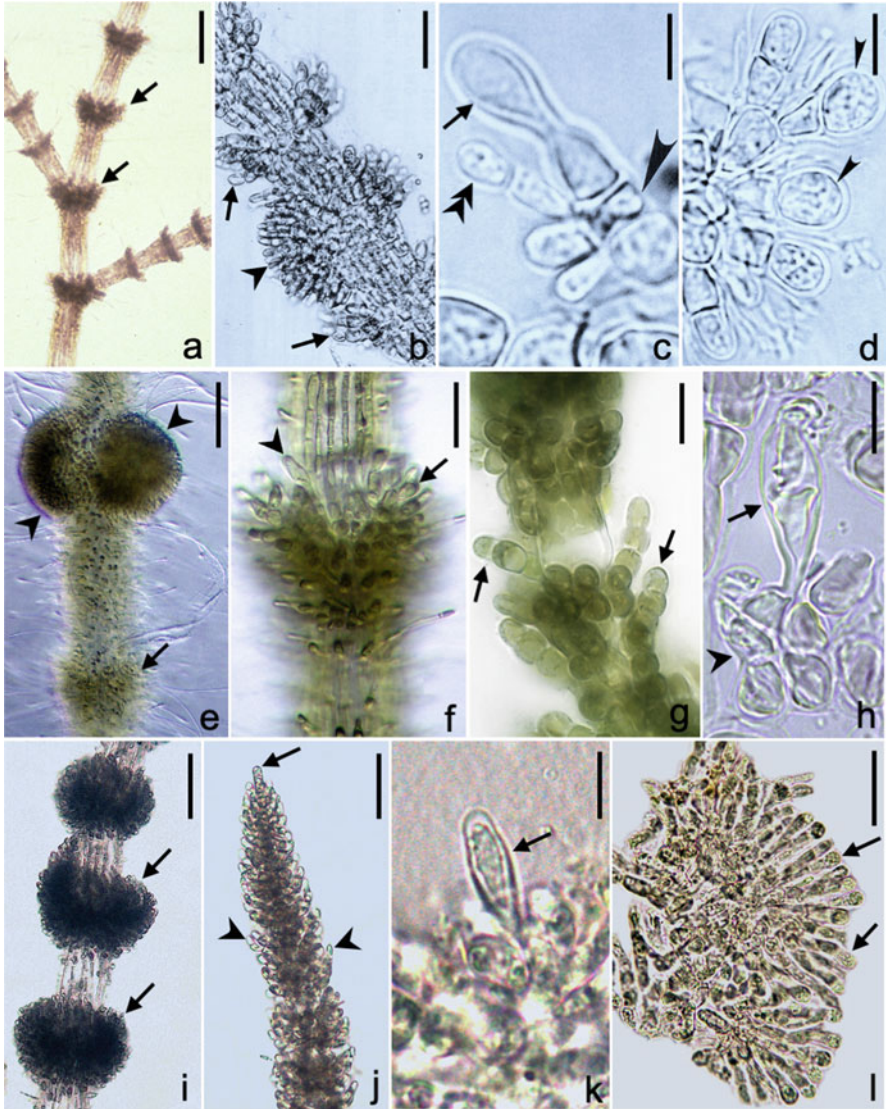
**Key reference:** Sheath et al. (1993).

***Torularia atra*** (Hudson) MJ Wynne, Notulae Algar 89:2 (2019) (Fig. 5.69e–h)

**Basionym:** *Conferva atra* Hudson, Fl Angl ed. 2:597 (1778).

**Homotypic synonyms:** *Batrachospermum atrum* (Hudson) Harvey, Man Brit Alg:120 (1841); *Nothocladus ater* (Hudson) Entwisle and ML Vis, J Phycol





**Fig. 5.69** (a–d) *Torularia androinvoluta*: (a) reduced whorls (arrows); (b) whorls with primary fascicles (arrows) and carposporophyte (arrowhead); (c) carpogonium with ellipsoidal trichogyne (arrow), carpogonial branch (arrowhead), and spermatangia on involucre filament (double arrowhead); (d) gonimoblast filaments with carposporangia (arrowheads); (e–h) *Torularia atra*: (e) reduced whorls (arrow) with carposporophytes (arrowheads); (f) reduced whorl with primary fascicle (arrow) and carpogonium (arrowhead); (g) young whorls with primary fascicles (arrows); (h) mature carpogonium with ellipsoidal trichogyne (arrow); (i–l) *Torularia atrobrasiliensis*: (i) reduced whorls (arrows); (j) plant tip with apical cell (arrow) and primary fascicles (arrowheads); (k) mature carpogonium with ellipsoidal trichogyne (arrow); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (a, e, i) = 100 μm; (b, f, j, l) = 50 μm (c, d, g, h, k) = 10 μm (Image authors: Fig. (e, f) P Eloranta; Fig. (g) C Carter. Fig. (b–d) reprinted with permission by Wiley from Sheath et al. (1993))

52:391 (2016); *Setacea atra* (Hudson) Necchi and NL Rossignolo, Phycologia 55:343 (2016); *Atrophycus ater* (Hudson) Necchi and NL Rossignolo, Notulae Algar 26:1 (2017).

**Type:** BM, Herb Sloane no. 229, D Brewer, prior to 1741 (Lectotype, Sheath et al. 1993).

**Type locality:** Wales, between Llanfaethly and Trefado, Gors Bach, 53.168167° N, 4.172944° W.

**Description:** thalli monoecious, dioecious, or polyecious; whorls not compact, contiguous or separated, obconic or pear-shaped, 70–290 µm in diameter; primary fascicles not adherent to each other and to axial and cortical cells, curved, unilaterally branched, with 3–7(–8) cells; secondary fascicles abundant and covering two-thirds to the entire, rarely one-third of the internode; spermatangia 4–8(–9.5) µm in diameter; carpogonial branches straight or slightly curved, composed of 2–5 disc- or barrel-shaped cells, developing from the periaxial or proximal cells of primary fascicles, short, 5–15 µm in length; carpogonia with sessile and clavate or ellipsoidal trichogynes, 15–33.5 µm in length, 4–7 µm in diameter; carposporophytes 1–2 per whorl, 70–240 µm in diameter and 50–175 µm in height; gonimoblast filaments with 2–6 barrel-shaped or cylindrical cells; carposporangia obovoidal or ellipsoidal, 7–14 µm in length and 5.5–11 µm in diameter.

**Diagnostic characters:** this species is similar in morphology to *T. atrobraziliensis* (distribution restricted to Brazil) and *T. meridionalis* (restricted to Australia) and is unequivocally distinguishable only by DNA sequence data, but geographic distribution can also be useful since it occurs in Africa, Asia, Australasia, and Europe.

**Representative sequences in GenBank:** KT894750 (COI-5P); AF029139, KM593813 (*rbcL*).

**Distribution:** Africa: South Africa; Asia: Japan; Australasia: Australia and New Zealand; Europe: Belgium, Finland, France, Germany, Latvia, Poland, Portugal, Spain, Sweden, Wales (Fig. 5.67). Distribution in Australia and New Zealand unclear due to difficulty separating this species from *T. meridionalis*.

**Key references:** Entwisle (1992), Sheath et al. (1993), Eloranta et al. (2011), Rossignolo and Necchi (2016).

*Torularia atrobraziliensis* MJ Wynne, Notulae Algar 89:3 (2019) (Fig. 5.69i–l)

**Type:** SJRP 31461, O Necchi Jr, 22.v.2008 (Holotype).

**Type locality:** Brazil, São Paulo State, Pindamonhangaba, 9 km from the entrance of Campos do Jordão State Park, 22.7225° S, 45.453611° W.

**Description:** thalli monoecious, dioecious or polyecious; whorls not compact, contiguous or separated, obconical or barrel-shaped, 170–425 µm in diameter; primary fascicles not adherent to each other and to axial and cortical cells, curved, with 3–8 cells; secondary fascicles abundant and covering two-thirds to the entire internode; spermatangia 6.5–9 µm in diameter; carpogonial branches straight or

slightly curved, composed of 3–5 disc- or barrel-shaped cells, developing from the periaxial or proximal cells of primary fascicles, 5–15  $\mu\text{m}$  in length; carpogonia with sessile, clavate, or ellipsoidal trichogynes, 21–30  $\mu\text{m}$  in length, 6.5–8  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, 95–235  $\mu\text{m}$  in diameter, and 50–185  $\mu\text{m}$  in height; gonimoblast filaments with 3–6 barrel-shaped or cylindrical cells; carposporangia obovoidal or ellipsoidal, 7–13  $\mu\text{m}$  in length, 7–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar in morphology to *T. atra* (widespread in Africa, Asia, Australasia, and Europe) and *T. meridionalis* (restricted to Australia) from which is unequivocally distinguishable only by DNA sequence data, but geographic distribution can also be useful since it is restricted to Brazil.

**Representative sequences in GenBank:** KT894748, KT894749 (COI-5P); KT183023, KT183024 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.67).

**Key references:** Rossignolo and Necchi (2016), Wynne (2019).

*Torularia meridionalis* ML Vis, Entwisle, and Necchi *sp. nov.* (Fig. 5.70a–d)

**Type:** WELT A027229 M.L Vis & S.A. Stewart, 10.xii.2004 (Holotype); BHO A-0016 (Isotype).

**Type locality:** New Zealand, South Island, Hokitika, stream near Loopline Road Scenic Reserve, 42.702222° S, 171.209167° E.

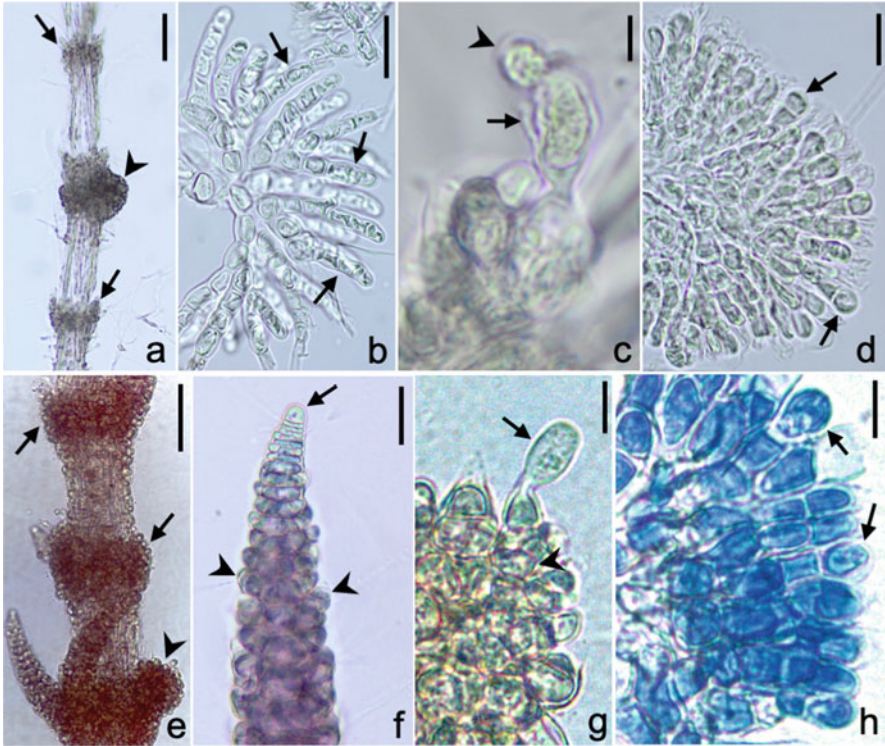
**Description:** thalli monoecious, dioecious or polyecious; whorls not compact, contiguous or separated, obconic or pear-shaped, 70–290  $\mu\text{m}$  in diameter; primary fascicles not adherent to each other and cortical cells, curved, unilaterally branched, with 3–7(–8) cells; secondary fascicles abundant and covering two-thirds, rarely one-third of the internode; spermatangia 4–8(–9.5)  $\mu\text{m}$  in diameter; carpogonial branches straight or slightly curved, composed of 2–5 disc- or barrel-shaped cells, developing on the periaxial or proximal cells of primary fascicles, 5–15  $\mu\text{m}$  in length; carpogonia with sessile and clavate or ellipsoidal trichogynes, 15–33.5  $\mu\text{m}$  in length, 6–8  $\mu\text{m}$  in diameter; carposporophytes 1–2 per whorl, 70–240  $\mu\text{m}$  in diameter, and 50–175  $\mu\text{m}$  in height; gonimoblast filaments with 2–6 barrel-shaped or cylindrical cells; carposporangia obovoidal or ellipsoidal, 7–14  $\mu\text{m}$  in length and 5.5–11  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar in morphology to *T. atro-brasiliensis* (distribution restricted to Brazil) and *T. atra* (cosmopolitan distribution in Africa, Asia, Australasia, and Europe). It can only be distinguished by DNA sequence data from *T. atra*, which overlaps in geographic range.

**Etymology:** the species epithet means southern and is applied because it is only known from Australia and New Zealand.

**Representative sequences in GenBank:** KT802756 (COI-5P); KT802840, KT802841(*rbcL*).

**Distribution:** Australasia: Australia, and New Zealand (Fig. 5.67). Distribution unclear due to difficulty separating this species from *T. atra*.



**Fig. 5.70** (a–d) *Torularia meridionalis*: (a) reduced whorls (arrows) with carposporophyte (arrowhead); (b) plant tip with apical cell (arrow) and compact primary fascicles (arrowheads); (c) mature carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Torularia puiggariana*: (e) reduced and compact whorls (arrows) with carposporophyte (arrowhead); (f) young carpogonium; (g) carpogonium with ellipsoidal trichogyne (arrow); (h) gonimoblast filaments with carposporangia (arrows). Scale bars: (a, e) = 100  $\mu\text{m}$ ; (f) = 50  $\mu\text{m}$ ; (b, d) = 20  $\mu\text{m}$ ; (g, h) = 10  $\mu\text{m}$ ; (c) = 5  $\mu\text{m}$

**Key reference:** Entwisle et al. (2016).

**Remarks:** this species formed a well-supported clade within *Torularia* (Entwisle et al. 2016, as *Nothocladus* section *Setaceus*) in a combined analysis based on five gene sequences (*rbcL*, LSU, COI-5P, *psaA*, and *psbA*) with high divergence from *T. atra* and is here proposed as a new species.

*Torularia puiggariana* (Grunow) MJ Wynne, Notulae Algar 89:2 (2019)  
(Fig. 5.70e–h)

**Basionym:** *Batrachospermum puiggarianum* Grunow in Wittrock and Nordstedt, Algae Exsicc 11:1, No. 501 (1883).



**Homotypic synonyms:** *Nothocladus puiggarianus* (Grunow) Entwisle and ML Vis, J Phycol 52:392 (2016); *Atrophycus puiggarianus* (Grunow) Necchi and NL Rossignolo, Notulae Algar 26:1 (2017).

**Type:** S A1545, YI Puiggari 1170, ix.1879 (Lectotype, here designated); RB 225281, S A1544 (Isolectotypes).

**Type locality:** Brazil, São Paulo State, Apiaí, 24.509722° S, 48.8425° W (estimated).

**Description:** thalli monoecious, dioecious, or polyecious; whorls compact, contiguous or separated, obconic or pear-shaped, 80–345 µm in diameter; primary fascicles adherent to each other and to cortical cells, curved, unilaterally branched, with 2–6 cells; secondary fascicles abundant and covering two-thirds to the entire, rarely one-third of the internode; spermatangia 4.5–7 µm in diameter; carpogonial branches straight or slightly curved, composed of 1–5 disc- or barrel-shaped cells, developing from the periaxial or proximal cells of primary fascicles, rarely on secondary fascicles or cortical filaments, 2–20 µm in length; carpogonia with sessile and clavate or ellipsoidal trichogynes, 17–32.5 µm in length, 5–9 µm in diameter; carposporophytes 1–2(–3) per whorl, 60–265(–305) µm in diameter and 45–220(–280) µm in height; gonimoblast filaments with 2–5(–6) barrel-shaped or short-cylindrical cells; carposporangia obovoidal or ellipsoidal, 7–13 µm in length and 5–11 µm in diameter.

**Diagnostic characters:** this species is distinguishable from others in the genus by the compact whorls with primary and secondary fascicles adherent to each other and to cortical cells.

**Representative sequences in GenBank:** KT894739, KT894744, KT894751 (COI-5P); KT183014, KT183019, KT894752 (*rbcL*).

**Distribution:** Africa: Angola; South America: Argentina, Brazil (Fig. 5.67).

**Key references:** Necchi (1990), Sheath et al. (1993), Rossignolo and Necchi (2016).

## Genus *Virescentia*

*Virescentia* (Sirodot) Necchi, DC Agostinho, and ML Vis, Cryptogam Algal 39:318 (2018)

**Basionym:** section *Virescentia* Sirodot, CR Acad Sci 76:1219 (1873).

**Synonyms:** section *Viridia* De Toni, Sylloge Floridearum, 60 (1897b); section *Vertis* Sirodot, Les Batrachospermes, 269 (1884); section *Claviformia* Reis, Bol Soc Brot 46:209 (1972b).

**Type species:** *V. helminthosa* (Bory) Necchi, DC Agostinho, and ML Vis, Cryptogam Algal 39: 321 (2018).



**Description:** plants monoecious, dioecious, or polyecious, greenish, greenish-blue, or less often brownish, consistency mucilaginous; branching irregular or less often pseudo-dichotomous; whorls well developed, contiguous or separated, obconic, pear-shaped, spherical or barrel-shaped; cortical filaments of the main axis well developed with cylindrical cells; primary fascicles formed by cells variable in shape and length the fascicle, ranging from cylindrical to ellipsoidal, obovoidal or pear-shaped or audouinelloid; secondary fascicles few and sparse to abundant and covering the entire internode; spermatangia on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, straight, rarely curved, developing from the periaxial or proximal cells of primary fascicles, rarely from distal cells of primary fascicles, secondary fascicles, or cortical filaments, short or long, composed of disc- or barrel-shaped cells; involucrel filaments, short, composed of cylindrical, ellipsoidal, or spherical cells; carpogonia with stalked, rarely shortly stalked, cylindrical, sub-cylindrical, clavate or ellipsoidal trichogynes; carposporophytes axial, hemispherical or spherical, inserted within the whorls, 1–2, rarely 3, per whorl, large; gonimoblast filaments densely arranged, composed of cylindrical, ellipsoidal, or barrel-shaped cells; carposporangia small or large, obovoidal, pear-shaped, clavate, or ellipsoidal.

**Diagnostic characters:** the genus is characterized by having carpogonial branches well differentiated from the fascicles, straight or slightly curved; carpogonia with stalked trichogynes; carposporophytes axial, centrally inserted within the whorls; and gonimoblast filaments of one type, densely arranged and arising radially from the fertilized carpogonia.

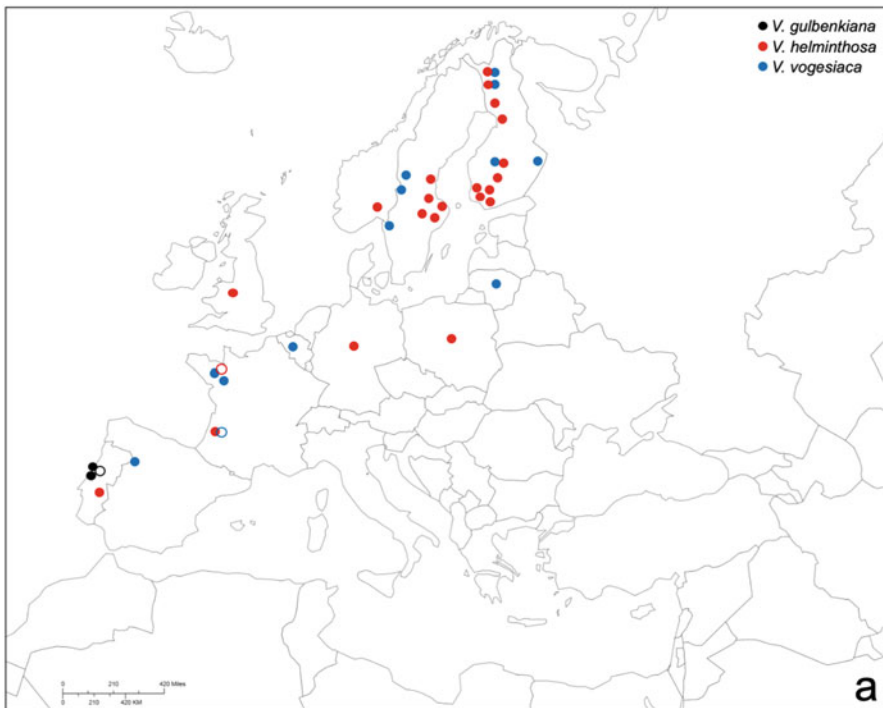
**Habitat:** species of *Virescentia* occur predominantly in unpolluted waters, with slightly acidic or circumneutral pH, low to moderate ion content, well aerated and moderate to fast flowing waters, rocky substrates, shaded or partly shaded stream segments.

**Distribution:** representatives of the genus have been reported in tropical, sub-tropical, and temperate regions of Asia, Europe, North and South America (Fig 5.71a, b).

**Phylogenetic relationships among species:** analyses of the *rbcL* sequences within the genus based on data reported by Necchi et al. (2018) revealed five clades with high support, corresponding to four geographic regions (Fig. 5.72): Asia (Japan), Europe (two clades), North America (USA) and South America (Brazil). Each clade represents a species, as follows: Asia (*Virescentia* sp.), Europe (*V. helminthosa* and *V. vogesiaca*), North America (*V. viride-americana*), and South America (*V. viride-brasiliensis*). There is a remaining sequence from Asia (Japan) that also represents a yet to be described distinct species, which brings the total number of species in the genus recognized using DNA sequence data to six. There are two species without sequence data (*V. crispata* and *V. gulbenkiana*) that are distinguished by morphology.

Key to the species of the genus *Virescentia*

1a	Whorls composed of curved and audouinelloid fascicles	<i>V. crispata</i>
1b	Whorls composed of straight and non-audouinelloid fascicles	2
2a	Carpogonial branches slightly curved	<i>V. helminthosa</i>
2b	Carpogonial branches straight	3
3a	Carpogonia short, 20–40 $\mu\text{m}$ in length, known distribution in Europe	4
3b	Carpogonia long, (35–)40–110 $\mu\text{m}$ in length, distribution restricted to the Americas	5
4a	Secondary fascicles few and sparse	<i>V. gulbenkiana</i>
4b	Secondary fascicles abundant and covering $\geq$ half of the internode length	<i>V. vogesiaca</i>
5a	Distribution restricted to North America (USA)	<i>V. viride americana</i>
5b	Distribution restricted to South America (Brazil)	<i>V. viride brasiliensis</i>



**Fig. 5.71** Map showing the distribution of *Virescentia* species: a) Europe—*V. gulbenkiana*, *V. helminthosa*, and *V. vogesiaca*; b) North and South America—*V. viride-americana* and *V. viride-brasiliensis*. Open symbols represent the type localities

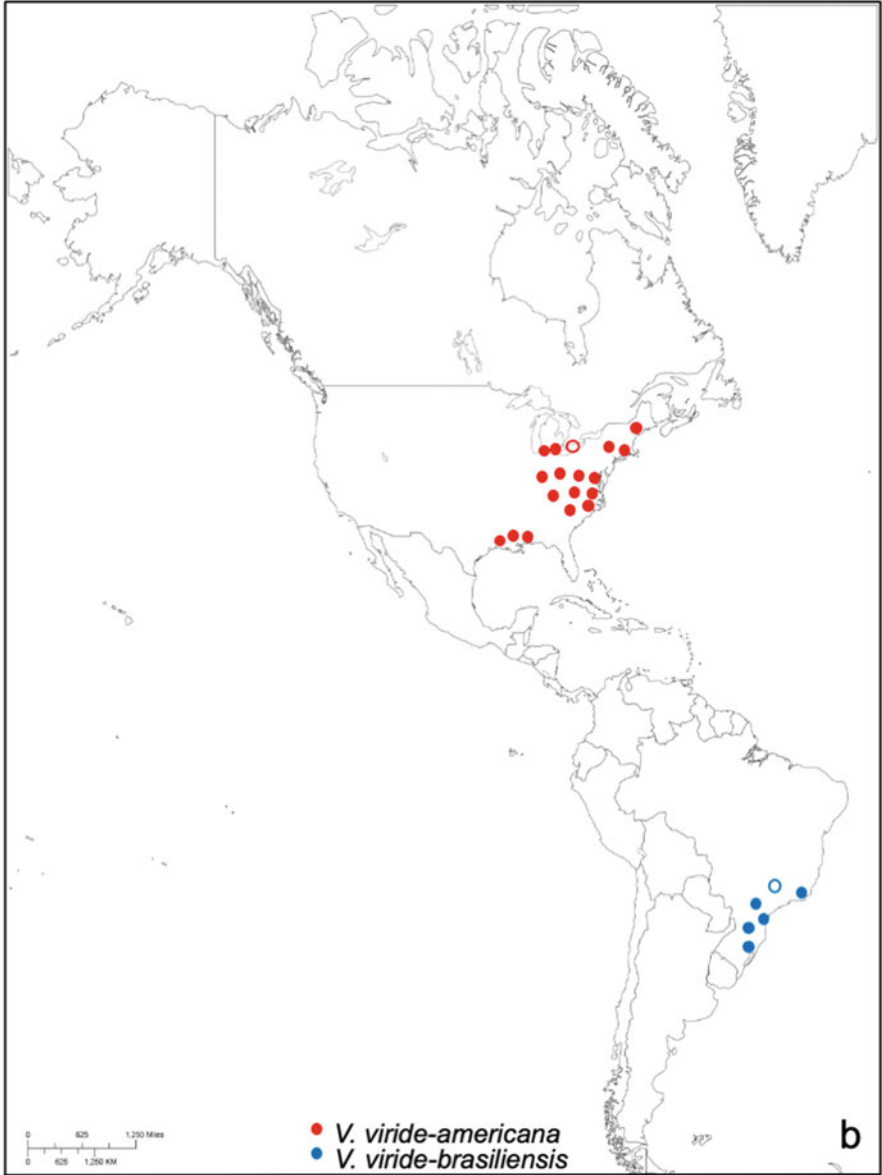
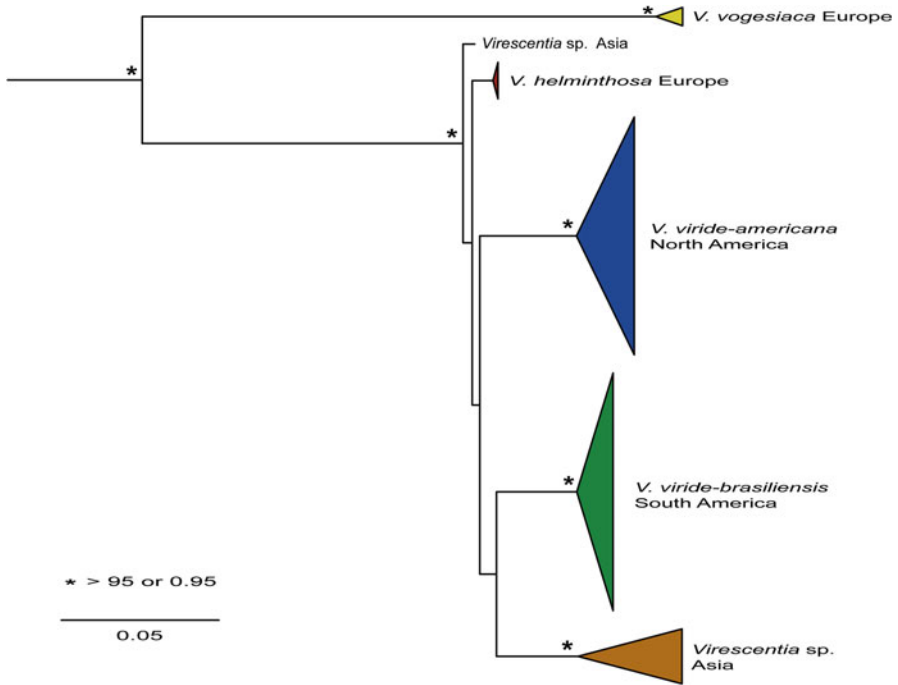


Fig. 5.71 (continued)



**Fig. 5.72** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Virescentia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities

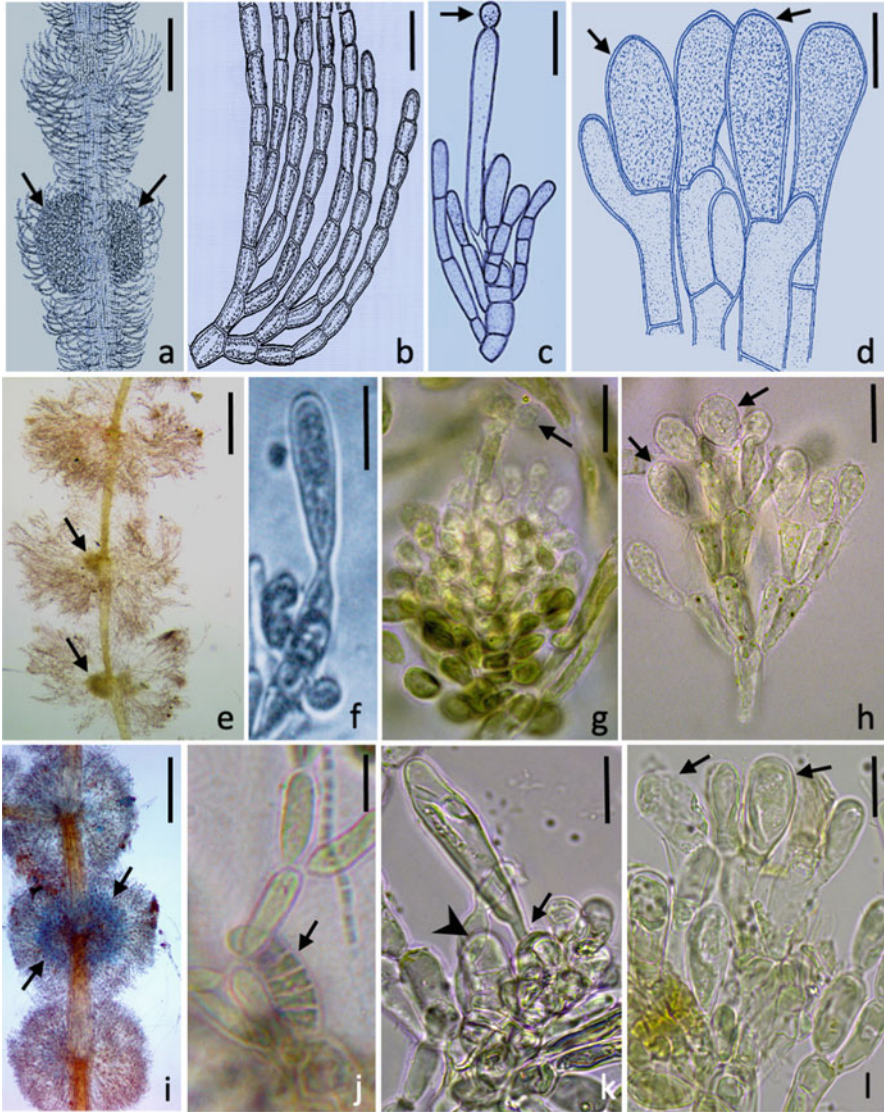
*Virescentia crispata* (Kumano and Ratnas) Necchi, DC Agostinho, and ML Vis, Cryptogam Algal 39: 319 (2018) (Fig. 5.73a–d)

**Basionym:** *Batrachospermum crispatum* Kumano and Ratnas, Jap J Phycol 30:18 (1982a).

**Type:** TNS-AL 169089, M Ratnasabapathy no. 21, 24.v.1974 (Isotype).

**Type locality:** Malaysia, Pulau Tioman, Sungai Ayer Besar, 02.790249° N, 104.169846° E (estimated).

**Description:** plants dioecious or polyecious; branching pseudodichotomous; whorls contiguous, obconic or pear-shaped, 150–350  $\mu\text{m}$  in diameter; primary fascicles curved, unilaterally branched, with 6–13 cells; secondary fascicles abundant and covering the entire internode; spermatangia spherical or obovoidal, on primary or secondary fascicles, 6–8  $\mu\text{m}$  in diameter; carpogonial branches slightly curved, composed of 3–4 disc- or barrel-shaped cells, developing from the periaxial or proximal cells of primary fascicles, short, 20–28  $\mu\text{m}$  in length; involucral filaments, short, composed of 2–4 cylindrical or elliptic cells; carpogonia 54–75  $\mu\text{m}$  in length, with stalked and cylindrical trichogynes; carposporophytes 1–2 per whorl, 140–300  $\mu\text{m}$  in diameter and 100–250  $\mu\text{m}$  in height; gonimoblast filaments with 3–5 cylindrical cells; carposporangia clavate or obovoidal, 14–30  $\mu\text{m}$  in length and 8–12  $\mu\text{m}$  in diameter.



**Fig. 5.73** (a–d) *Virescentia crispata*: (a) whorls with carposporophytes (arrows); (b) primary fascicle; (c) carpogonium with cylindrical trichogyne and attached spermatium (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Virescentia gulbenkiana*: (e) whorls with carposporophytes (arrows); (f) young carpogonium; (g) carpogonium with cylindrical trichogyne and attached spermatium (arrow); (h) gonimoblast filaments with carposporangia (arrows); (e–h) *Virescentia helminthosa*: (i) whorls with carposporophytes (arrows); (j) young carpogonial branch (arrow); (k) carpogonium with clavate and stalked (arrow) trichogyne and a young carpogonial branch (arrowhead); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (e, i) = 250 µm; (a) = 100 µm; (b–d, f–h, j–l) = 10 µm (All figures reprinted with permission by the Publications Scientifiques du Muséum National d’Histoire Naturelle, Paris, from Necchi et al. (2018))



**Diagnostic characters:** this species is unique in the genus due to the presence of audouinelloid, curved, and unilaterally branched primary and secondary fascicles.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Malaysia.

**Key references:** Ratnasabapathy and Kumano (1982a), Kumano (2002), Necchi et al. (2018).

*Virescentia gulbenkiana* (Reis) Necchi, DC Agostinho, and ML Vis, *Cryptogam Algal* 39:319 (2018) (Fig. 5.73e–h)

**Basionym:** *Batrachospermum gulbenkianum* Reis, *Anu Soc Brot* 31:31 (1965a).

**Type:** COI, MP Reis and A Santos, no. 456, 07.vii.1965 (Holotype).

**Type locality:** Portugal, Confulcos, River Águeda, 40.688728° N, 08.144225° W.

**Description:** plants monoecious or polyecious; branching irregular; whorls contiguous or separated, barrel-shaped or spherical, 430–810 µm in diameter; primary fascicles straight, with 8–13 cells; secondary fascicles few and sparse; spermatangia spherical, on primary fascicles, 4–6 µm in diameter; carpogonial branches straight, composed of 3–12 disc-shaped cells, developing from the periaxial or proximal cells of primary fascicles, short or long, 9–35 µm in length; involucrel filaments, short, composed of 1–3 cylindrical or elliptic cells; carpogonia 20–39 µm in length, with stalked, clavate, or cylindrical trichogynes; carposporophytes 1–3 per whorl, 120–300 µm in diameter, and 60–150 µm in height; gonimoblast filaments with 2–5 cylindrical cells; carposporangia obovoid or pear-shaped, 10–18 µm in length, 6.5–10 µm in diameter.

**Diagnostic characters:** this species is distinguishable from the other species occurring in Europe by the few and sparse secondary fascicles, straight carpogonial branches, and short carpogonia.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Europe: Portugal (Fig. 5.71a).

**Key references:** Reis (1965a, 1967, 1972b, 1974), Kumano (2002), Necchi et al. (2018).

*Virescentia helminthosa* (Bory) Necchi, DC Agostinho, and ML Vis, *Cryptogam Algal* 39:321 (2018) (Fig. 5.73i–l)

**Basionym:** *Batrachospermum helminthosum* Bory, *Ann Mus Hist Nat* 12:316 (1808b).

**Type:** PC0591734, Bory de St. Vincent, no collection date (Lectotype).

**Type locality:** France, near Fougères, 48.351561° N, 01.204626° W (estimated).

**Description:** plants monoecious or polyecious; branching irregular; whorls contiguous or separated, barrel-shaped, spherical, or pear-shaped, 300–800 µm in diameter; primary fascicles straight, with 8–15 cells; secondary fascicles varying from few and sparse to abundant and covering the entire internode; spermatangia spherical, on primary or secondary fascicles, 5–7 µm in diameter; carpogonial branches slightly curved, composed of 3–11 disc-shaped cells, developing from the periaxial, proximal, or distal cells of primary fascicles or cortical filaments of

the main axis, short or long, 12–35  $\mu\text{m}$  in length; involucrel filaments, short, composed of 1–3 cylindrical, ellipsoidal, or spherical cells; carpogonia 40–79  $\mu\text{m}$  in length, with stalked, cylindrical trichogynes, sometimes bifurcated or with knobs; carposporophytes 1–2 per whorl, 150–420  $\mu\text{m}$  in diameter, 100–320  $\mu\text{m}$  in height; gonimoblast filaments with 3–7 cylindrical cells; carposporangia obovoid or pear-shaped, 14–20.5  $\mu\text{m}$  in length, 8.5–12.5  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinguishable from the other species of the genus occurring in Europe by the slightly curved carpogonial branches.

**Representative sequences in GenBank:** HQ412541, HQ412542 (COI-5P); KJ825955, KM593807, KM593841 (*rbcL*).

**Distribution:** Europe: Finland, France, Norway, Poland, Portugal, Sweden (Fig. 5.71a).

**Key references:** Sirodot (1884), Israelson (1942), Reis (1974), Eloranta et al. (2011), Chiasson et al. (2014), Necchi et al. (2018).

**Remarks:** this species has been reported in other regions of the world but based on the current taxonomic circumscription and DNA sequence data it is only known to occur in Europe.

*Virescentia viride-americana* Necchi, DC Agostinho, and ML Vis, Cryptogam  
Algol 39: 321 (2018) (Fig. 5.74a–d)

**Type:** BHO A-1174, ML Vis and RG Verb, 29.v.1998 (Holotype).

**Type locality:** the USA, Big Run, Ohio, 4.2 miles east on Big Run Road (CR8S) from SR 329, 39.353813° N, 81.842615° W.

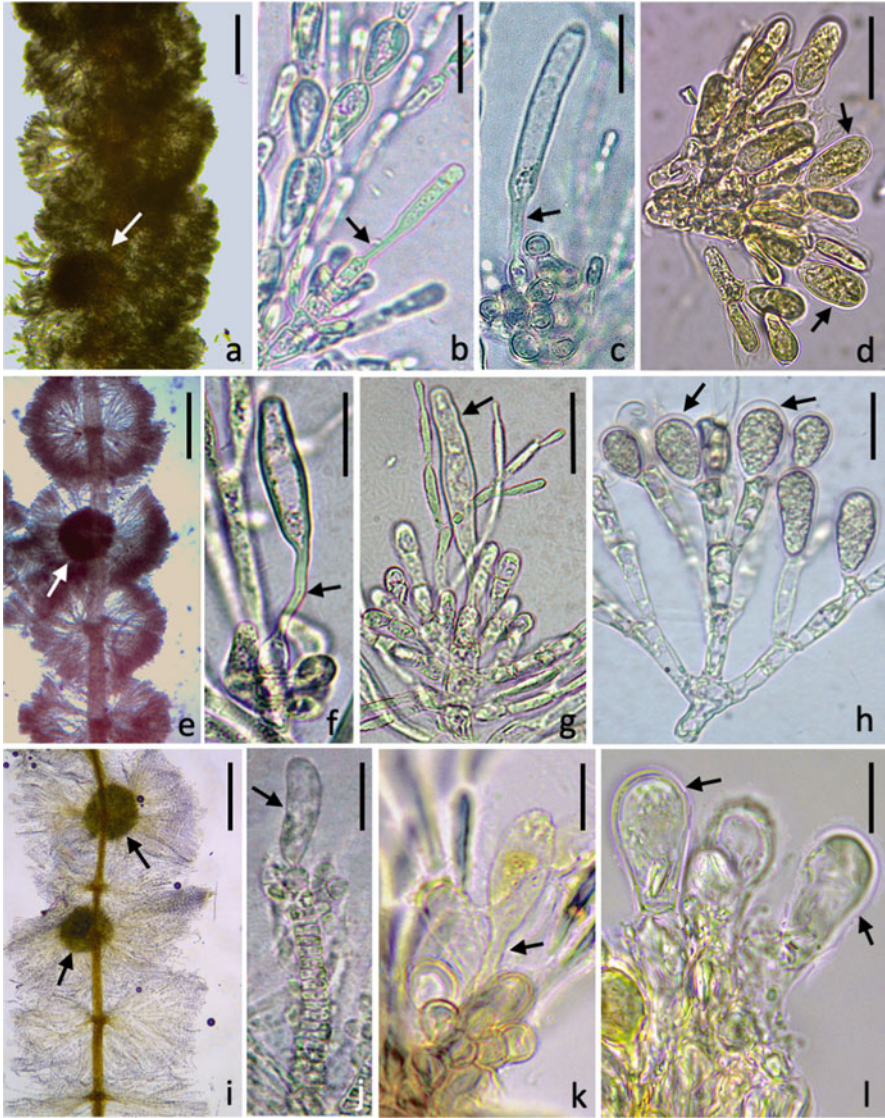
**Description:** plants monoecious, dioecious, or polyecious; branching irregular; whorls contiguous or separated, barrel-shaped, spherical, or pear-shaped, 280–940  $\mu\text{m}$  in diameter; primary fascicles straight, with 8–19 cells; secondary fascicles varying from few and sparse to abundant and covering the entire internode; spermatangia spherical, on primary or secondary fascicles, 4–8  $\mu\text{m}$  in diameter; carpogonial branches straight, composed of 1–7 disc-shaped cells, developing from the periaxial or proximal cells of primary fascicles, short or long, 6–30  $\mu\text{m}$  in length; involucrel filaments, short, composed of 1–3 cylindrical or ellipsoidal cells; carpogonia (30–)40–77  $\mu\text{m}$  in length, with stalked, clavate, or cylindrical trichogynes; carposporophytes 1–2 per whorl, (130–)140–390  $\mu\text{m}$  in diameter, 70–200(–240)  $\mu\text{m}$  in height; gonimoblast filaments with 3–5 cylindrical cells; carposporangia obovoid or pear-shaped, 15–24  $\mu\text{m}$  in length, 8–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is similar in morphology to *V. viride-brasiliensis*, but it is distinguished based on divergences in DNA sequences (COI-5P and *rbcL*) and for the known geographic distribution with occurrence only in North America.

**Representative sequences in GenBank:** EU073845, EU073846, EU636736 (COI-5P); AF244110, AF244117, AF244118 (*rbcL*).

**Distribution:** North America: the USA (Fig. 5.71b).

**Key references:** Sheath et al. (1994a), Vis et al. (2001), Necchi et al. (2018).



**Fig. 5.74** (a–d) *Virescentia viride-americana*: (a) whorls with carposporophytes (arrows); (b) young carpogonium with stalked trichogyne (arrow); (c) carpogonium with cylindrical and stalked trichogyne (arrow); (d) gonimoblast filaments with carposporangia (arrows); (e–h) *Virescentia viride-brasiliensis*: (e) whorls with carposporophyte (arrow); (f) young carpogonium with stalked trichogyne (arrow); (g) carpogonium with clavate trichogyne (arrow); (h) gonimoblast filaments with carposporangia (arrows); (e–h) *Virescentia vogesiaca*: (i) whorls with carposporophytes (arrows); (j) carpogonium with stalked trichogyne; (k) young carpogonium with ellipsoidal and stalked trichogyne (arrow); (l) gonimoblast filaments with carposporangia (arrows). Scale bars: (e, i) = 250 µm; (a) = 100 µm; (b–d, f–h, j–l) = 10 µm (All figures reproduced with permission by the Publications Scientifiques du Muséum National d’Histoire Naturelle, Paris, from Necchi et al. (2018))

*Virescentia viride-brasiliensis* Necchi, DC Agostinho, and ML Vis, Cryptogam Algal 39: 325 (2018) (Fig. 5.74e–h)

**Basionym:** *Batrachospermum viride-brasiliense* Necchi and DC Agostinho, Phycologia 53:566 (2014).

**Type:** SJRP 29845, MO Paiano, 15.xii.2009 (Holotype); SP 428881 (Isotype).

**Type locality:** Brazil, São Paulo State: Campos do Jordão, ‘Ducha da Prata’, 22.738056° S, 45.569444° W.

**Description:** plants monoecious, dioecious, or polyecious; branching irregular; whorls contiguous or separated, barrel-shaped, spherical, pear-shaped, or obconic, 280–1100 µm in diameter; primary fascicles straight, with 7–18 cells; secondary fascicles varying from few and sparse to abundant and covering the entire internode; spermatangia spherical or obovoid, on primary or secondary fascicles, 4–9 µm wide; carpogonial straight, short, composed of 1–7 disc-shaped cells, developing from the periaxial or proximal cells of primary fascicles, short or long, 4–37.5 µm long; involucrel filaments, short, composed of 1–3 cylindrical or spherical cells; carpogonia 40–110 mm long, with stalked, clavate or sub-cylindrical trichogynes; carposporophytes 1–2 per whorl, 200–550 µm in diameter, and 100–300 µm in height; gonimoblast filaments with 3–6 cells cylindrical or barrel-shaped cells; carposporangia obovoid, pear-shaped, or elliptic, 19–35 µm in length, 10–24 µm in diameter.

**Diagnostic characters:** this species resembles *V. viride-americana* in all morphological features, but it can be distinguished by the divergence in sequences of *rbcL* and COI-5P and the disjunct geographic distribution (restricted to Brazil).

**Representative sequences in GenBank:** KX452188, KX452196 (COI-5P); KM097031, KM097042 (*rbcL*).

**Distribution:** South America: Brazil (Fig. 5.71b).

**Key references:** Necchi (1990), Agostinho and Necchi (2014), Necchi et al. (2018).

*Virescentia vogesiaca* (TG Schultz ex Skuja) Necchi, Agostinho, and ML Vis, Cryptogam Algal 39:325 (2018) (Fig. 5.74i–l)

**Basionym:** *Batrachospermum vogesiacum* TG Schultz ex Skuja, Arch Hydrobiol Suppl 15:623 (1938).

**Type:** PC0591499, S Sirodot, 01.viii.1880 (Lectotype).

**Type locality:** France, Laugerie-Haute, 44.952526° N, 01.001166° E (estimated).

**Description:** plants monoecious; branching irregular; whorls contiguous or separated, barrel-shaped, obconic, pear-shaped, or spherical, 340–700 µm in diameter; primary fascicles straight, with 7–14 cells; secondary fascicles abundant, covering half to the entire internode; spermatangia spherical, on primary or secondary fascicles, 5–8 µm in diameter; carpogonial branches straight, composed of (4–) 8–20 disc-shaped cells, developing from the periaxial or proximal cells of primary fascicles, long or short, (13–)25–68 µm in length; involucrel filaments, short, composed of 1–3 ellipsoidal or spherical cells; carpogonia 20–45 µm in diameter, with stalked or shortly stalked, clavate or ellipsoidal trichogynes; carposporophytes 1–2 per whorl, 140–330 mm wide, 95–175 mm high; gonimoblast filaments with 4–7 cylindrical or ellipsoidal cells; carposporangia obovoidal, 13–19 µm in length, 8.5–13 µm in diameter.

**Diagnostic characters:** this species is distinguishable from the other European species of the genus by the abundant secondary fascicles and the straight carpogonial branches.

**Representative sequences in GenBank:** KJ825953, KU754497(*rbcL*).

**Distribution:** Europe: Belgium, Finland, France, Latvia, Spain, Sweden (Fig. 5.71a).

**Key references:** Sirodot (1884), Israelson (1942), Eloranta et al. (2011), Chiasson et al. (2014), Necchi et al. (2018).

## ***Virescentia* spp.**

As commented above, there are two distinct species from Japan that are recognizable based on *rbcL* sequence analysis (Fig. 5.72), which were reported as *B. helminthosum* by Hanyuda et al. (2004). However, according to Hanyuda (pers comm) there are no vouchers to be examined to describe the morphological characters of those specimens to propose a new species. Until a formal proposal is pursued, the status of these Japanese materials remains unresolved.

## **Genus *Visia***

*Visia* Necchi, Phytotaxa 395:57 (2019b)

**Synonyms:** section *Aristata* Skuja ex Kumano, Jap J Phycol 41:262 (1993) (= section “*Aristatae*” Skuja, Arch Protistenkd 80:364 (1933); sub-section *Aristatae* Kumano, Jap J Phycol 41:262 (1993).

**Type species:** *Visia cayennensis* (Montagne) Necchi and AS Garcia, Phytotaxa 395: 57 (2019b).

**Description:** plants monoecious, dioecious, or polyecious, greenish, greenish-blue, or less often brownish, consistency mucilaginous; branching irregular; whorls well developed, contiguous or separated, barrel-shaped, obconic, or spherical; cortication of the main thallus axis well developed with filaments of cylindrical cells; primary fascicles formed by non-audouinelloid cells, ranging from cylindrical to elliptical, obovoid or spherical, or audouinelloid cells (cylindrical or barrel-shaped) in a single species; secondary fascicles abundant and covering half to the entire internode or few and sparse in a single species; spermatangia spherical or obovoidal, on primary or secondary fascicles; carpogonial branches well differentiated from the fascicles, straight or slightly curved, typically long, developing from the periaxial, rarely from proximal cells of primary fascicles, composed of disc-, barrel-shaped or cylindrical cells; involucrel filaments long (proximal part) or short (distal part), composed of cylindrical, ellipsoidal, fusiform, barrel-shaped, obovoidal, or sub-spherical cells; carpogonia with unstalked,



clavate or elongate-clavate, rarely undulated trichogynes; carpogonia becoming swollen and divided endogenously after fertilization in one species; carposporophytes pedunculate or short-pedunculate, spherical or sub-spherical, 1–3 per whorl, small; gonimoblast filaments densely arranged, composed of cylindrical or barrel-shaped cells; carposporangia obovoidal or clavate.

**Diagnostic characters:** the genus is characterized by having well-developed whorls, carpogonial branches that are well-differentiated from the fascicles, straight or slightly curved and usually long; carposporophytes pedunculate, spread in the whorls at various heights; gonimoblast filaments of one type, densely arranged and arising radially from the fertilized carpogonia.

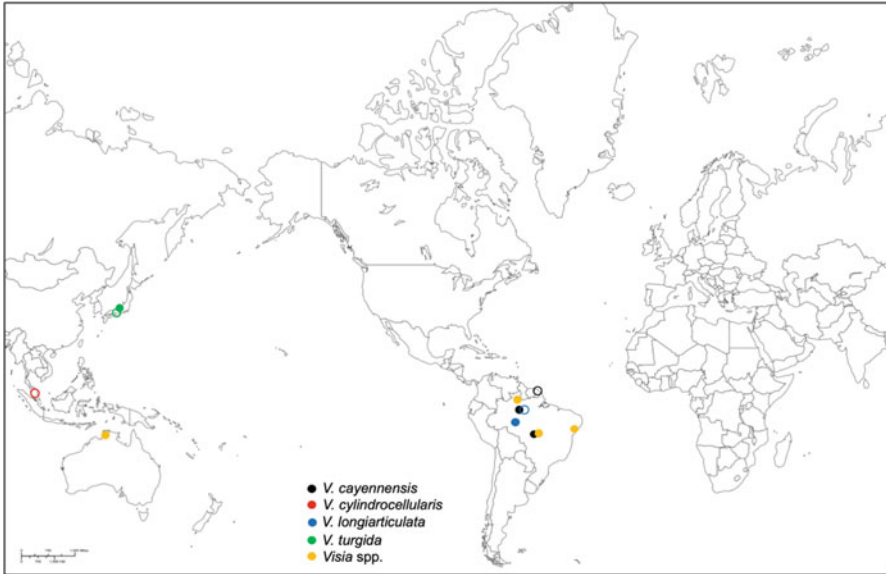
**Habitat:** species of *Visia* occur predominantly in waters with relatively high temperatures ( $\geq 24$  °C), mildly acidic (pH 5.7–6.2), low ion content ( $8\text{--}60\ \mu\text{S cm}^{-1}$ ), moderately to fast flowing ( $44\text{--}93\ \text{cm s}^{-1}$ ), yellow to dark brown color in partly shaded streams or rivers, attached to macrophytes or fallen tree trunks, less often on rocky substrata (Johnston et al. 2014; Necchi unpublished data).

**Distribution:** representatives of the genus have been reported in tropical regions of Asia, Australasia, and South America (Fig. 5.75).

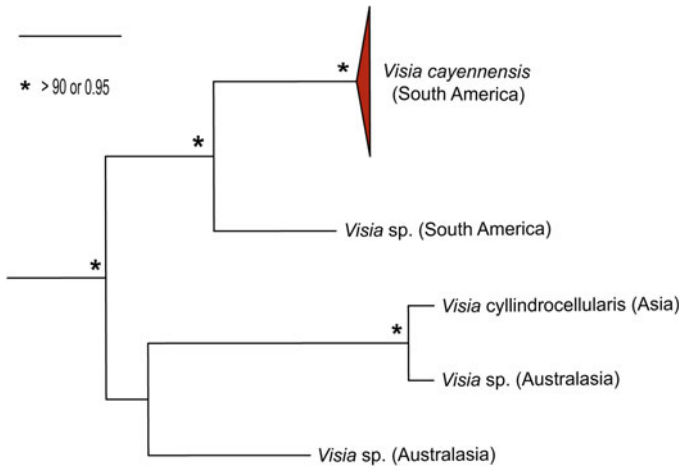
**Phylogenetic relationships among species:** analyses of the *rbcL* sequences within the genus based on data reported in the most recent study (Necchi et al. 2019b) showed *Visia* as a monophyletic group with high support and two subclades (Fig. 5.76): one with *V. cayennensis* and *Visia* sp. from South America (Brazil and French Guiana); and another with *V. cylindrocellularis* from Asia (Malaysia) and *Visia* sp. from Australasia (Australia). Another sequence of *Visia* sp. from Australasia (Australia) was on a long branch, sister to this latter clade. These sequences reported as *Visia* spp. are morphologically very similar to *V. cayennensis* but genetically very divergent. These *rbcL* data are supported by COI-5P sequences (Necchi et al. 2019a) and indicate that there is a substantial genetic diversity and cryptic species within *Visia* requiring further investigation. There are two species without sequence data (*V. longiarticulata* and *V. turgida*) that are distinguished by morphology.

Key to the species of the genus *Visia*

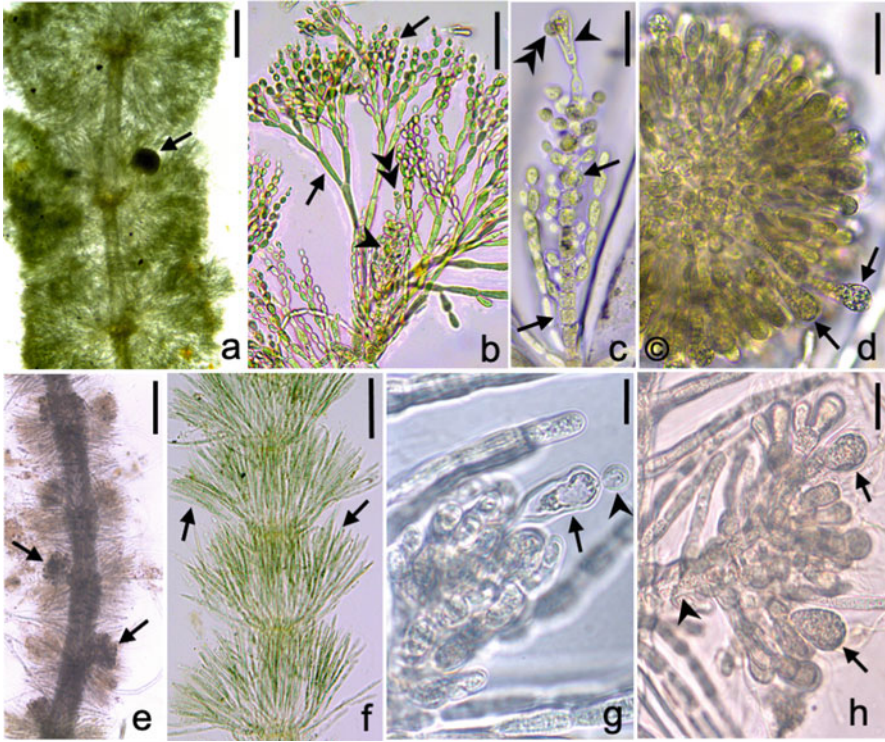
1a	Whorls composed of audouinelloid fascicles, exclusively with cylindrical cells, unilaterally branched	<i>V. cylindrocellularis</i>
1b	Whorls composed of non-audouinelloid fascicles, with cylindrical, ellipsoidal, obovoidal, or spherical cells, di- or trichotomously branched	2
2a	Carpogonial branches $\leq 70\ \mu\text{m}$ in length; carpogonia becoming swollen and dividing endogenously after fertilization	<i>V. turgida</i>
2b	Carpogonial branches $\geq 80\ \mu\text{m}$ in length; carpogonia not becoming swollen and not dividing endogenously after fertilization	3
3a	Primary fascicles $\geq 20$ cells; secondary fascicles few and sparse	<i>V. longiarticulata</i>
3b	Primary fascicles $< 20$ cells; secondary fascicles abundant and covering half to the entire internode	<i>V. cayennensis</i>



**Fig. 5.75** Map showing the distribution of *Visia* species. Open symbols represent the type localities



**Fig. 5.76** Maximum Likelihood tree based on *rbcL* sequences showing the phylogenetic relationships among the species of *Visia*. Support values are maximum likelihood bootstrap and Bayesian posterior probabilities



**Fig. 5.77** (a–d) *Visia cayennensis*: (a) whorls with carposporophyte (arrow); (b) primary fascicles (arrows), carpogonial branch (arrowhead) and carpogonium (double arrowhead); (c) carpogonial branch (arrows) with clavate trichogyne (arrowhead); (d) carposporophyte with carposporangia (arrows); (e–h) *Visia cylindrocellularis*: (e) whorls with carposporophytes (arrows); (f) whorls with audouinelloid and curved fascicles (arrows); (g) fertilized carpogonium with clavate trichogyne (arrow) and attached spermatium (arrowhead); (h) developing carposporophyte with carposporangia (arrows). Scale bars: (a) = 250  $\mu\text{m}$ ; (e) = 200  $\mu\text{m}$ ; (f) = 100  $\mu\text{m}$ ; (b) = 50  $\mu\text{m}$ ; (c, d) = 25  $\mu\text{m}$ ; (g, h) = 10  $\mu\text{m}$  (Fig. (d) reproduced with permission from Magnolia Press (copyright holder) from Necchi et al. (2019a))

*Visia cayennensis* (Montagne) Necchi and AS Garcia, *Phytotaxa* 395:57 (2019b) (Fig. 5.77a–d)

**Basionym:** *Batrachospermum cayennense* Montagne in Kütz, *Spec Algar* 537 (1849).

**Type:** PC0452172, Herbarium Montagne, FMR Leprieur 348 (Holotype); PC0452173-0452175, Herbarium Montagne; PC0591478, PC0591485, PC0591486, Herbarium Thuret; PC0658115-PC0658117, PC0658066-PC0658069, Herbarium Rest of the World (Isotypes).

**Type locality:** French Guiana, Cayenne, 04.922420° N, 52.313453° W (estimated).

**Description:** plants monoecious, dioecious, or polyecious; whorls contiguous or separated, barrel-shaped, obconical, or spherical, 600–2300 µm in diameter; primary fascicles straight, with 10–17(–19) cells; secondary fascicles abundant, covering half to the entire internode; spermatangia 4–8 µm in diameter; carpogonial branches straight, composed of 8–30 cells, developing from the periaxial of primary fascicles, (80–)110–270 µm in length; carpogonia 25–44 µm in length, 9–13 in diameter; carposporophytes 80–220(–285) µm in diameter; gonimoblast filaments with 2–5(–6) cylindrical cells; carposporangia obovoidal or clavate, (11–)13.5–20 µm in length, (6–)8–12 µm in diameter.

**Diagnostic characters:** this species is distinct from others in the genus by the combination of non-audouinelloid primary fascicles with <20 cells, abundant secondary fascicles half to the entire internode and long carpogonial branches (≥8 cells and ≥80 µm in length).

**Representative sequences in GenBank:** EU636726, MH917722 (COI-5P); AY423392, AY423393 (*rbcL*).

**Distribution:** South America: Brazil, French Guiana (Fig. 5.75).

**Key references:** Necchi (1990), Sheath et al. (1994b), Kumano (2002), Necchi et al. (2019b).

*Visia cylindrocellularis* (Kumano) Necchi and AS Garcia, Phytotaxa 395:59 (2019b) (Fig. 5.77e–h)

**Basionym:** *Batrachospermum cylindrocellulare* Kumano, Bot Mag Tokyo 91: 100 (1978).

**Type:** TNS-AL 169083, S Kumano, 16.iv.1971 (Holotype); TNS-AL 169080 (Isotype).

**Type locality:** Malaysia, Pahang, Fort Iskander, Tasek Bera, 03.006344° S, 102.615370° E.

**Description:** plants monoecious; whorls contiguous, barrel-shaped or obconical, 300–450 µm in diameter; primary fascicles audouinelloid, curved, unilaterally branched, with 7–12 cells; secondary fascicles abundant and covering the entire internode; spermatangia 4–8 µm in diameter; carpogonial branches straight, composed of 12–22 cells, developing from the periaxial or proximal cells of primary fascicles, 120–250 µm in length; carpogonia 17–35 µm in length, 6–9 µm in diameter; carposporophytes 100–150 µm in diameter; gonimoblast filaments with 2–4 cylindrical or barrel-shaped cells; carposporangia clavate or obovoidal, 11–15 µm in length and 8–12 µm in diameter.

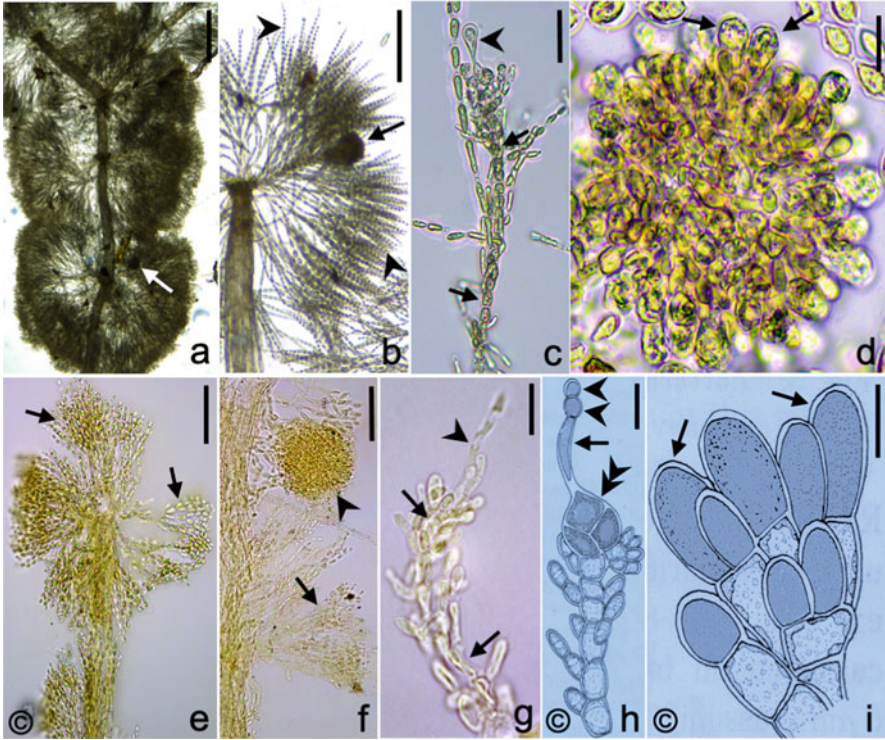
**Diagnostic characters:** this species is unique in the genus by the presence of curved audouinelloid fascicles (exclusively with cylindrical cells).

**Representative sequences in GenBank:** KF557568 (*rbcL*).

**Distribution:** Asia: Malaysia (Fig. 5.75).

**Key references:** Kumano (1978, 2002), Necchi et al. (2019b).





**Fig. 5.78** (a–d) *Visia longiarticulata*: (a) whorls with carposporophyte (arrow); (b) part of whorl with pedunculate carposporophyte (arrow) and primary fascicles (arrowheads); (c) carpogonial branch (arrows) with clavate trichogyne (arrowhead); (d) carposporophyte with carposporangia (arrows); (e–i) *Visia turgida*: (e) whorl with primary fascicles (arrows); (f) part of whorl with primary fascicle (arrow) and pedunculate carposporophyte (arrowhead); (g) carpogonial branch (arrows) and carpogonium with clavate and undulated trichogyne (arrowhead); (h) fertilized carpogonium with elongate-clavate trichogyne (arrow), attached spermatia (arrowheads) and endogenous divided carpogonium (double arrowhead); (i) gonimoblast filaments with carposporangia (arrows). Scale bars: (a) = 250  $\mu\text{m}$ ; (e) = 100  $\mu\text{m}$ ; (f) = 50  $\mu\text{m}$ ; (c) = 25  $\mu\text{m}$ ; (d, g–i) = 10  $\mu\text{m}$  (Fig. (e, h, i) reproduced with permission by Magnolia Press from Necchi et al. (2019a))

*Visia longiarticulata* (Necchi) Necchi and AS Garcia, *Phytotaxa* 395:59 (2019b) (Fig. 5.78a–d)

**Basionym:** *Batrachospermum longiarticulatum* Necchi, *Bibl Phycol* 84:31 (1990).

**Type:** SP187156, O Necchi Jr, 29.i.1984, O Necchi Jr, 22 May 2008 (Holotype; Isotype 32169).

**Type locality:** Brazil, Amazonas, Presidente Figueiredo, Route BR-174, km 115, 02.030007° S, 60.026047° W.

**Description:** plants monoecious; whorls contiguous or separated, barrel-shaped or spherical, 1100–2400  $\mu\text{m}$  in diameter; primary fascicles with 20–32 cells; secondary fascicles few and sparse; spermatangia 5–7  $\mu\text{m}$  in diameter; carpogonial



branches straight, composed of 10–25 cells, developing from the periaxial cells of primary fascicles, 120–250  $\mu\text{m}$  in length; carpogonia 22–33.5  $\mu\text{m}$  in length, 7–10  $\mu\text{m}$  in diameter; carposporophytes 75–160  $\mu\text{m}$  in diameter; gonimoblast filaments with 2–5 cylindrical or barrel-shaped cells; carposporangia obovoidal or clavate, 12.5–18  $\mu\text{m}$  in length and 6.5–10  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is distinct from others in the genus by the combination of non-audouinelloid primary fascicles with  $\geq 20$  cells, few and sparse secondary fascicles and long carpogonial branches ( $\geq 10$  cells and  $\geq 120$   $\mu\text{m}$  in length).

**Representative sequences in GenBank:** no sequences available.

**Distribution:** South America: Brazil (Fig. 5.75).

**Key references:** Necchi (1990), Sheath et al. (1994b), Necchi et al. (2019b).

*Visia turgida* (Kumano) Necchi and AS Garcia, Phytotaxa 395:62 (2019b) (Fig. 5.78e–i)

**Basionym:** *Batrachospermum turgidum* Kumano, Jap J Phycol 930:291 (1982b).

**Type:** TNS-AL 169087, R Seto, 11.v.1958 (Holotype; Isotype TNS-AL 169221).

**Type locality:** Japan, Mie, Mount Gozaisyo-dake, Kita-dani, 35.011247° N, 136.420016° E.

**Description:** plants monoecious or polyecious; whorls contiguous or separated, barrel-shaped or spherical, 350–500  $\mu\text{m}$  in diameter; primary fascicles straight, with 7–15 cells; secondary fascicles few and sparse; spermatangia 4.5–7  $\mu\text{m}$  in diameter; carpogonial branches straight or slightly curved, composed of 5–8 cells, developing from the periaxial cells of primary fascicles, 40–70  $\mu\text{m}$  in length; carpogonia with undulated trichogynes, becoming swollen and dividing endogenously after fertilization, 30–50  $\mu\text{m}$  in length, 3–6  $\mu\text{m}$  in diameter; carposporophytes 120–210  $\mu\text{m}$  in diameter; gonimoblast filaments with 2–4 cylindrical cells; carposporangia obovoidal or ellipsoidal, 16–20  $\mu\text{m}$  in length and 8–12  $\mu\text{m}$  in diameter.

**Diagnostic characters:** this species is unique in the genus by the fertilized carpogonium becoming swollen and divided endogenously.

**Representative sequences in GenBank:** no sequences available.

**Distribution:** Asia: Japan (Fig. 5.75).

**Key references:** Kumano (1982b, 2002), Necchi et al. (2019b).

## *Visia* spp.

As commented above, there are three species from Australasia (Australia) and South America (Brazil) that are morphologically similar to *V. cayennensis* but highly divergent for COI-5P and *rbcL* sequences (Fig. 5.76). The status of these species requires further investigation and formal proposal of new species within the genus.

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## Appendix: Recent Articles That Could not be Included in the Book

The articles listed below were published after we had finished the respective sections in which they would be referenced or after we had submitted the book. Therefore, that information was not included in the book content.

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