Revision of *Batrachospermum* section *Macrospora* (Batrachospermales, Rhodophyta) with the establishment of the new genus *Montagnia*

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Running title: Revision of *Macrospora* (Batrachospermales) and *Montagnia* gen. nov.

ABSTRACT: In order to resolve the paraphyly of *Batrachospermum*, the sections of the genus have been methodically investigated using DNA sequence data and morphology resulting in the raising of many sections to genus status. Phylogenetic analyses of combined *rbc*L and COI-5P showed *Batrachospermum* section *Macrospora* to be a well-supported clade. We propose to raise this section to genus level as *Montagnia* gen. nov. *Montagnia* is distinguished from other sections or genera of the Batrachospermales by the following characters: plants irregularly branched; carpogonial branches well-differentiated from the fascicles, long and straight, bearing involucral filaments in a crown-pattern; enlarged pit-connections in the cells of the carpogonial branches; pedunculate carposporophytes with large carposporangia. Within the new genus, we re-evaluated the characters used to circumscribe species by examining type specimens as well as samples from North and South America. Of the three currently accepted species attributable to the genus *Montagnia*, we recognized two species: *M. macrospora* – type species (proposed synonyms *Batrachospermum equisetifolium, B. hypogynum* and *B. macrosporum*) and *M. australis* (synonym *Batrachospermum australe*). Morphological characters available for species identification did not distinguish between the two species due to variation in characters within and among samples. The two species can only be differentiated using DNA sequence data and geographic distribution. *Montagnia australis* is restricted to North America, whereas *M. macrospora* is a widespread pantropical species occurring in South America and Asia. Although the intra-specific divergence observed in *M. macrospora* is the highest reported for members of the Batrachospermales, the species delimitation methods did not suggest that more than one species is justified.

KEY WORDS: Batrachospermales, biogeography, COI-5P, freshwater red algae, *rbc*L gene, molecular systematics, morphology, Rhodophyta, taxonomy

INTRODUCTION

The first phylogenetic study to focus on the freshwater red algal order Batrachospermales determined the genus *Batrachospermum* to be paraphyletic with the infrageneric sections variously related to other genera of the order (Vis *et al.* 1998). Subsequent research has expanded the sampling of taxa with DNA sequence data and established new genera for many of the sections of *Batrachospermum.* The genera *Kumanoa* (former sections *Contorta* and *Hybrida*), *Sheathia* (former section *Helminthoidea*) *Torularia* (= *Atrophycus*, former section *Setacea*), *Virescentia* (formerly a section with the same name) and *Acarposporophycos* (former section *Acarposporophytum*) and *Visia* (former section *Aristata*) have been circumscribed and the species belonging to them delineated (Entwisle *et al.* 2009; Necchi & Vis 2012; Salomaki *et al*. 2014; Rossignolo & Necchi 2016; Necchi *et al.* 2018, 2019). In addition, the new genera *Lympha* (Evans *et al.* 2017), *Nocturama* (Entwisle *et al*. 2016) and *Volatus* (Chapuis *et al*. 2017) have been recently proposed in the order. Section *Macrospora* is one of the few remaining sections in need of revision to resolve the paraphyly of *Batrachospermum sensu lato.*

Section *Macrospora* was first proposed as a separate taxonomic entity by Kumano (1993) who recognized it as one of two subsections within section *Aristata*. It was later split from section *Aristata* and raised to section status based on DNA sequence data (Entwisle *et al*. 2009). This section includes species of the genus *Batrachospermum* with the following characters: plants irregularly branched, carpogonial branches well-differentiated from the fascicles, long and straight bearing involucral filaments with a rosette-like arrangement, symmetrical carpogonia and pedunculate carposporophytes with large carposporangia (Ratnasabapathy & Kumano 1982; Kumano 1990; Necchi 1990; Sheath *et al*. 1994; Entwisle & Foard 1997; Kumano 2002; Vis *et al*. 2004). Kumano & Necchi (1990) examined Brazilian populations and the type specimen of *B. macrosporum* providing details of carpogonium and carposporophyte development, as well as carpospore germination. They described the presence of hypogynous cells forming rosette-like laterals and enlarged protoplasmic connections between the carpogonium and the hypogynous cells. Kumano (1990) described the characteristics of carpogonia and carposporophytes of two species of the section: *B. equisetifolium* and *B. macrosporum.* Based on the examination of type specimens, Sheath *et al*. (1994) placed *B. australe* Collins (1906), *B. excelsum* Montagne (1850) and *B. oxycladum* Montagne (1850) in synonym with *B. macrosporum*. Sheath *et al.* (1994) compared morphological characters of representative type specimens and populations in North America and concluded that there were few morphometric characters to distinguish species and recognized a single geographically widespread species, *B. macrosporum* Montagne (1850), as well as the geographically restricted *B. hypogynum* Kumano & Ratnasabapathy (Ratnasabapathy & Kumano 1982). Currently, three species are recognized within the section, *B. equisetifolium* Montagne (1850), *B. hypogynum* and *B. macrosporum*, which are distinguished by number of cells of carpogonial branches and size of the carpogonia and the carposporangia (Kumano 2002).

To date, there have been a few studies that have provided DNA sequence data for section *Macrospora*. Vis *et al.* (1998) included DNA sequence data from the SSU (small subunit rDNA) and *rbc*L (plastid-encoded RuBisCO large subunit) for specimens from Mississippi, USA. Subsequently, Vis *et al.* (2005) provided *rbc*L sequences for specimens of *B. macrosporum* from rivers in French Guiana near the type locality for the species. A phylogeographic study of *B. macrosporum* in North and South America using the mitochondrial intergenic spacer between the cytochrome oxidase subunit 2 and 3 genes (*cox*2-3) showed a wide divergence between the North American and South American locations (Vis *et al*. 2008). For the North American locations, there were few base pair differences among the eight haplotypes, but among the eight haplotypes from South America there was more population structure and base pair differences. These results between continents and among locations were reflected in the *rbc*L sequence data as well (Vis *et al*. 2008). Although morphology was examined, no morphological differences could be discerned at that time among the intraspecific groups revealed in the analyses. Likewise, Sherwood *et al.* (2008) reported a high sequence divergence for the barcode region of the mitochondrial gene encoding cytochrome oxidase subunit 1 (COI-5P) among specimens from North and South America. The sequences for the three markers (*rbc*L, *cox*2-3 spacer and COI-5P), showed the same pattern for intra and interspecific divergences. Recently, *rbc*L sequence data for *B. macrosporum* have been published for locations in Asia (Taiwan and Malaysia) (Chou *et al*. 2014; Johnston *et al*. 2014).

Species delineation within the Batrachospermales is typically based on characters from gametophytic stage, whereas the sporophytic 'Chantransia' stage usually has little or no value to discriminate species (Necchi 1990; Sheath *et al*. 1994; Entwisle & Foard 1997; Kumano 2002). However, there are three morphologically distinct form taxa of 'Chantransia': 'C. richardsii', 'C. pygmaea' and 'C. macrospora' (Vis *et al*. 2006). 'C. richardsii' (= *Ptilothamnion richardsii* Skuja) has been associated with *Kumanoa* sp. and *Nocturama antipodites* (Entwisle) Entwisle & M.L. Vis (Vis *et al*. 2006). Numerous studies have shown that many Batrachospermales species are linked with 'Chantransia pygmaea' (= *A. pygmaea* (Kützing) Weber Bosse) (Chiasson *et al*. 2005, 2007; Necchi & Oliveira 2011; Johnston *et al*. 2014). Of note and unlike the other 'Chantransia' forms, investigations of 'C. macrospora' [= *Audouinella macrospora* Wood (Sheath & Burkholder)] have all showed this form taxon to be exclusively linked, via DNA sequence data, to *B. macrosporum* (Chiasson *et al*. 2005; Kato *et al*. 2009; Necchi & Oliveira 2011; Johnston *et al.* 2014).

Taxonomic studies relying on morphological characters have demonstrated few diagnostic characters useful for species delineation in section *Macrospora* (Ratnasabapathy & Kumano 1982; Necchi 1990; Sheath *et al*. 1994; Entwisle & Foard 1997; Kumano 2002). In contrast, studies focused on phylogeography and specimen identification using DNA sequence data have indicated that there is considerable genetic variation, particularly for *B.*

macrosporum (Chiasson *et al*. 2005; Vis *et al*. 2005, 2008; Sherwood *et al*. 2008; Necchi & Oliveira 2011). Therefore, in this study, we aim to bring together morphological and DNA sequence data to inform the systematics of the species within section *Macrospora* and to investigate the phylogenetic relationship with other sections/genera of Batrachospermales. We conducted this revision by analyzing the DNA sequence data of two markers (*rbc*L and COI-5P) of specimens from three continents (North and South Americas and Asia) to evaluate the taxonomic status of the section. In addition, we examined the morphology of type specimens and samples from North and South America to circumscribe species.

MATERIAL AND METHODS

Morphological data were gleaned for type specimens and collections attributable to species in the section *Macrospora* (Ratnasabapathy & Kumano 1982; Kumano 1990; Kumano & Necchi 1990; Necchi 1990; Sheath *et al*. 1994; Kumano 2002). In addition, type specimens of the three species assigned to section *Macrospora* (Kumano 2002) were newly examined (Table S1). The morphology of specimens from North America and Brazil with previous DNA sequence data was also analyzed (Vis *et al*. 2008) (Table S2, Supporting information). Lastly, we examined eleven new samples collected in Brazil for which morphology and DNA sequence data were obtained for this study (Table S2). Specimens analyzed in this and previous investigations are lodged at herbaria BHO and SJRP (Thiers 2019). The synonyms listed for each species are all designated in this study. Morphological and morphometric characters considered diagnostic for species of the section in relevant taxonomic literature were evaluated (Ratnasabapathy & Kumano 1982; Kumano 1990; Kumano & Necchi 1990; Necchi 1990; Sheath *et al*. 1994; Kumano 2002). For observations and measurements, we followed the same procedures described our previous studies (Vis *et al*. 2008; Agostinho & Necchi 2014; Rossignolo & Necchi 2016; Necchi *et al*. 2018).

For the eleven new specimens from Brazil, DNA extraction, PCR amplification, PCR product purification and Sanger sequencing followed the protocols described previously (Vis *et al*. 2008; Agostinho & Necchi 2014; Rossignolo & Necchi 2016; Necchi *et al*. 2018). Two markers were sequenced: the plastid-encoded RuBisCO large-subunit gene (*rbc*L) and the barcode region of the mitochondrial encoded cytochrome *c* oxidase subunit 1 (COI-5P). Four specimens for which *rbc*L was available from a previous study had the COI-5P PCR amplified and sequenced using the protocols described in Salomaki *et al*. (2014).

For phylogenetic analyses of the *rbc*L and combined *rbc*L + COI-5P sequence data, a GTR + I + G was used as the best-fit model of sequence evolution as determined by the Akaike Information Criterion using jModelTest 2.1.4 (Darriba *et al*. 2012). Single gene (*rbc*L) analyses were conducted and a combined analysis for specimens from which both markers were available. Maximum likelihood (ML) topologies and bootstrap values from 10,000 replicates were inferred using RAxML_GUI version 1.5 (Silvestro & Michalak 2012). Bayesian analysis (BA) was performed in MrBayes 3.2 (Ronquist & Huelsenbeck 2003) with three runs of five chains of Metropolis coupled Markov Chain Monte Carlo for 1 x10^6 generations. 500,000 chains were removed as burn-in prior to determining the posterior probabilities. For COI-5P, a neighbor-joining analysis was conducted with support values determined from 10,000 replications executed in Geneious ver. 10 (www.geneious.com).

Two species delimitation methods were used to support decisions regarding the number of species within the section. Both the *rbc*L and COI-5P sequences were explored for barcode gaps, a clear distinction between inter- vs intraspecific variation (Leliaert *et al.* 2014). The Automatic Barcode Gap Discovery (ABGD) program was utilized via the ABGD website (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) (Puillandre *et al.* 2012). Species Delimitation (SD) analysis (Masters *et al.* 2011) was applied to evaluate whether or not minor groups could be discriminated within major groups in a gene tree. These analyses were performed using the SD plugin in Geneious.

RESULTS

Molecular analyses

Nine previously unpublished *rbc*L sequences were combined with 27 unique sequences of *B. macrosporum* or 'Chantransia macrospora' and representatives of all Batrachospermales genera and *Batrachospermum* sections and Thoreales. Both the BA and ML analyses resulted in the same tree topology so only the ML tree is shown (Fig. 1). Many of the generic and section clades received strong bootstrap support, but the relationships among them were not always well-supported. There was strong or moderate support (> 90% bootstrap and 0.90 posterior probability) for the monophyly of section *Macrospora* (Fig. 1). Within the section *Macrospora* clade, there were two strongly supported groups (Table S2, Fig. 1): a small clade with sequences from North America (USA) and a larger clade with sequences from South America (Bolivia, Brazil and French Guiana) and Asia (Japan, Malaysia and Taiwan). Likewise, these two groups emerged with a clear gap in the ABGD analysis (Fig. S1) and well-supported in the SD analysis (Table S3, Fig. S2). The interspecific variation between these two groups was high (68-90 bp, 5.3–7.0%), whereas sequence divergence within a group was low for the group of USA sequences (1-5 bp, 0.1-0.4%) and higher for the South America/Asia clade (0-90 bp, 0-7%). Despite the high sequence divergence, there was no support to split the South America/Asia sequences into more than one species in either the ABGD or SD analyses (Table S3, Fig. S1).

Fourteen new sequences of COI-5P were generated in this study and combined with 16 sequences from GenBank. Neighbor-joining analysis for COI-5P sequences (Fig. S2) showed one well-supported group with samples from North America (USA) and a large group with moderate support for samples from South America and Asia. These two groups were shown with clear gaps in the ABGD analysis (Fig. S3) and high support in the SD analysis (Table S4). High interspecific divergences were observed between these two groups (59-69 bp, 8.9-

10.4%), whereas the variation within a group was low for the USA sequences (0-10 bp, 0-1.5%) and wide for the group with South America and Asia sequences (0-54 bp, 0–8.1%). Like the results for *rbc*L data, ABGD and SD results showed no support to discriminate more than one species within the South America/Asia group (Table S4, Fig. S3).

The combined analysis of *rbc*L and COI-5P sequence data included 15 specimens of section *Macrospora* and representatives (48) of most Batrachospermales taxa (Table S5). Both the BA and ML analyses resulted in the same tree topology so only the ML tree is shown (Fig. 2). Most generic and section clades had high support, but the relationships among them were mostly not well supported. Section *Macrospora* was strongly supported as a clade and contained two subclades: one containing the populations from North America (USA) and the other with specimens from South America (Bolivia, Brazil and French Guiana).

Morphological analyses

Eleven samples and three type specimens were analyzed for vegetative and reproductive characters (Tables S6-S7, Figs 3–22). Among these specimens, a wide and continuous variation in morphological and morphometric characters was observed. Overall, most specimens showed plants irregularly branched having obconic whorls with pedunculate carposporophytes (65-211 μm in diameter); carposporangia large (21-65 μm in length, 15-42 μm in diameter); carpogonia short to long (28-72 μm in length); trichogynes club-shaped or pear-shaped, sessile or pedicellate; carpogonial branches typically long (4-21 cell layers, 35-275 μm in length). We observed that North American specimens tended to have longer carpogonia and smaller carposporangia than the South American samples (Table S7): carpogonia mean ranges 45.6-63.1 versus 32.8-43.8 mm in length; and carposporangia means 29.0-32.2 versus 38.5-56.0 mm in length and 23.0-26.1 versus 25.5-34.0 mm in diameter, respectively. However, the overall ranges in values overlapped considerably among populations of the two continents.

Two characters were consistently observed in all specimens examined. Wider pit-connections were present in the cells of carpogonial branches (Figs 9, 21). Post-fertilization stages revealed pit-connections considerably enlarged (Figs 11-14). In addition, upper involucral cells developed around the carpogonium in a crown-like pattern (Figs 8, 11, 19-20).

DISCUSSION

Two species were recognized based on DNA sequence data, one is restricted to North America and the other is from South America and Asia. Our results corroborated the phylogeographic findings by Vis *et al.* (2008) that showed a distinct dichotomy between specimens of *B. macrosporum* collected in locations from North and South America, respectively. Despite the high sequence divergence, no morphological differences were apparent between the specimens from the two continents so no taxonomic proposal was made, although the authors did not rule out cryptic speciation. Like the previous studies using DNA sequence data, this study showed little variation between sequences from North American specimens (Sherwood *et al.* 2008; Vis *et al.* 2008). However, among specimens from South America there is higher sequence divergence (≤ 7% for *rbc*L and ≤ 10% for COI-5P) similar to the findings in previous studies (Sherwood *et al.* 2008; Vis *et al.* 2008). The sequence data from Asia did not expand the divergence even though they add greatly to the geographic range of the species. These intra-specific sequence divergences are the greatest reported within the Batrachospermales to date (Table S8), which is probably associated with the widespread global distribution of *B. macrosporum*.

The geographic range for *B. australe* and *B. macrosporum* are distinct. Populations attributed to *B. australe* from North America occur predominantly in the southeastern coastal plain (Sheath *et al.* 1994; Vis *et al.* 2008), with some records (including many as ‘Chantransia macrospora’) extending to other biomes (deciduous forest, tropical rainforest and hemlockhardwood forest, Sheath & Cole 1990; Necchi *et al*. 1993). On the other hand, samples of *B. macrosporum* from South America and Asia suggest a pantropical distribution (Necchi 1990; Sheath *et al*. 1994; Vis *et al.* 2005, 2008; Kato *et al*. 2009; Chou *et al*. 2014; Johnston *et al*. 2014) and this species as being one of the most widespread among the Batrachospermales. If the records of 'Chantransia macrospora' are considered in addition to the gametophytes, this species is not only widespread, but also very abundant in most sites where it is found (Sheath & Hambrook 1990; Necchi *et al.* 1999). The 'Chantransia' stage is usually associated with population maintenance due to its tolerance to wide environmental variation (Hambrook & Sheath 1991; Necchi 1993), including photosynthetic characteristics (Necchi & Alves 2005). This is a highly adaptive strategy of members of Batrachospermales to lotic habitats (Sheath & Hambrook 1990) and can explain the widespread occurrence of this species.

Unlike the high sequence divergence observed between populations of North America in comparison to those from South America and Asia, the morphological characters showed no clear distinction among these two species. In the analyses of this study and previous investigations, many of the morphological characters showed continuous and wide variation within and between samples from both groups (Necchi 1990; Sheath *et al*. 1994; Entwisle & Foard 1997; Kumano 2002; Vis *et al*. 2004). Thus, the two species recognized based on DNA sequence data and geographic differences could not be distinguished by morphological characters. The results of this study confirm the conclusion by Sheath *et al*. (1994) that there is a lack of morphometric characters to distinguish species. The characters applied by Kumano (2002) to distinguish three species within section *Macrospora* (number of cells of carpogonial branches and size of the carpogonia and the carposporangia) are shown to be of no taxonomic values. Our observations confirmed the presence of characters usually attributed to this section in all specimens examined of section *Macrospora*: plants irregularly branched; carpogonial branches well-differentiated from the fascicles, long and straight, bearing involucral filaments in a crown-pattern (rosette-like arrangement); symmetrical carpogonia and pedunculate carposporophytes with large carposporangia (Ratnasabapathy & Kumano 1982; Necchi 1990; Sheath *et al.* 1994; Entwisle & Foard 1997; Kumano 2002; Vis *et al.* 2004). Of note is the presence of an additional character for all members of the section, the occurrence of enlarged pit-connections in the cells of the carpogonial branches. This character is clearly distinguishable in mature carpogonial branches, and had been described in Brazilian populations and the type specimen of *B. macrosporum* (Kumano & Necchi 1990). However, unlike that study we have not interpreted the presence the cells subtending the carpogonia bearing involucral cells arranged in a crown-pattern as hypogynous cells. Hypogynous cells have been observed in some more complex red algae (Hommersand & Fredericq 1990), and are cells which fuse with the carpogonia at early stages of the carposporophyte development. We have not observed such fusion of the subtending cells of the carpogonial branch with the carpogonia after fertilization.

The molecular and morphological findings discussed here have important taxonomic implications leading to changes and new proposals that are described in detail below.

TAXONOMIC TREATMENT

Genus *Montagnia* Necchi, M.L. Vis & A.S. Garcia, gen. nov.

Synonyms: Section *Macrospora* (Necchi) Entwisle, M.L.Vis, W.B.Chiasson, Necchi & A.R.Sherwood 2009, p. 713; **Section *Aristata* Subsection *Macrospora*** Kumano 1993, p. 263.

Revised description: plants monoicous, dioicous or polyoicous; branching irregular; whorls well-developed; cortication of the main thallus axis composed of one or two layers of filaments with cylindrical cells; primary fascicles composed of cylindrical to ellipsoidal, obovoid or spherical cells with 5-12 cell layers; secondary fascicles abundant and covering half to the entire internode; spermatangia spherical or obovoid, on primary or secondary fascicles; carpogonial branches well-differentiated from the fascicles, straight, developing from the periaxial or from proximal cells of primary fascicles, rarely on cortical filaments, long, composed of 4-16 barrel-shaped or short-cylindrical cells, 40-260 µm long; involucral filaments composed of 1-10 cells, with distal cells forming a crown around the carpogonia; carpogonia, short or long, 28-72 µm long, with sessile or pedicellate, club or pear-shaped trichogynes; fertilized carpogonia and subtending cells of carpogonial branches with enlarged pit-connections; carposporophytes pedunculate, spherical, contained within the whorls, 1-3 per whorl, small, 80-285 µm in diameter; gonimoblast filaments densely arranged, composed of 2–5 cylindrical or barrel-shaped cells; carposporangia obovoid, pear-shaped, large, 24-66 µm long, 16-45 µm wide.

Type species: *Montagnia macrospora* (Montagne) Necchi, M.L. Vis & A.S. Garcia, comb. nov.

Etymology: the genus name honors C. Montagne (1784-1866), French botanist, who played an important role in the genus history, particularly by proposing the type species. The section name *Macrospora* is not applicable for a genus name according to Article 20.2 of the International Code for Nomenclature of Algae, Fungi and Plants (Turland *et al*. 2018), since it coincides with a Latin technical term in use in morphology and would not be validly published. In addition, the combination of the type species (*Batrachospermum macrosporum*) would result in a tautonym (*Macrospora macrospora*), which is not allowed according to Article 23.4 of the Code.

Montagnia macrospora (Montagne) Necchi, M.L. Vis & A.S. Garcia, comb. nov.

Figures 3–14

Basionym: *Batrachospermum macrosporum* Montagne 1850, p. 293.

Revised description: Plants monoicous, dioicous or polyoicous, abundantly to moderately mucilaginous, bluish or blue-greenish; branching irregular; whorls contiguous or separated, barrel-shaped, obconical, pear-shaped or spherical, 500–2,500 µm wide; primary fascicles straight, with 5-10(-12) cell layers; proximal cells cylindrical or ellipsoidal, distal cells obovoid, sub-spherical or spherical; secondary fascicles abundant, covering half to the entire internode; cortication of the main thallus axis composed of one or two layers of filaments with cylindrical cells; monosporangia obovoid or pear-shaped, on distal cells of primary and secondary fascicles; spermatangia spherical or obovoid, on primary or secondary fascicles, 5–11 µm in diameter; carpogonial branches composed of 4-12(-16) barrel-shaped or short-cylindrical cells, developing from the periaxial cells, proximal cells of primary fascicles or on carpogonial branches, rarely from cortical filaments, (40-)60-200(-260) µm long; involucral filaments composed of 1-10 ellipsoidal or fusiform proximal cells and usually 1-2 club-shaped, sub-spherical or ellipsoidal distal cells forming a crown around the carpogonia; carpogonia 28–50 µm long, with sessile or pedicellate, club- or pear-shaped trichogynes; fertilized carpogonia and subtending cells of carpogonial branches with enlarged pit-connections; carposporophytes pedunculate spherical or sub-spherical, contained within the whorls, 1-3(-4) per whorl, small, 80-220(-285) µm in diameter; gonimoblast filaments densely arranged, composed of 2–5 cylindrical or barrel-shaped cells; carposporangia obovoid or pear-shaped, 30-66 µm long, 20-45 µm wide.

Distribution: South America (Bolivia, Brazil, French Guiana) (Necchi 1990, this study) and Asia (Japan, Malaysia, Taiwan).

Additional specimens examined: Brazil: Amazonas, Bahia, Mato Grosso, Roraima, São Paulo (Table S1).

Representative DNA sequences: EU636750, **MK532360**, MK304453 (COI-5P); AY423415, MK304442, MK304441 (*rbc*L).

Remarks: monosporangia on fascicle cells of the gametophytes are here reported for the first time in this species, which is an additional mode of dispersal. Monosporangia have been observed on the gametophytes in few species of *Kumanoa* (Necchi & Vis 2012), the section *Turfosa* of *Batrachospermum* (Kumano 2002) and *Batrachospermum* sensu stricto (Vis *et al*. 1996; Chapuis *et al*. 2017).

Montagnia australis (Collins) Necchi & M.L.Vis, comb. nov.

Figures 15-22

Basionym: *Batrachospermum australe* Collins 1906, p. 110.

Revised description: Plants monoicous, dioicous or polyoicous, abundantly to moderately mucilaginous, bluish or blue-greenish; branching irregular; whorls contiguous or separated, barrel-shaped, obconical, pear-shaped or spherical, 390–1,160 µm wide; primary fascicles straight, with (4-)6-8(-10) cell layers; proximal cells cylindrical or ellipsoidal, distal cells cylindrical, obovoid or sub-spherical; secondary fascicles abundant, covering half to the entire internode; cortication of the main thallus axis composed of one or two layers of filaments with cylindrical cells; spermatangia spherical or obovoid, on primary or secondary fascicles, 4.5–10 µm in diameter; carpogonial branches composed of 4-13 barrel-shaped or short-cylindrical cells, developing from the periaxial cells or proximal cells of primary fascicles or sometimes on carpogonial branches, (47-)60-100(-156) µm long; involucral filaments composed of 1-10 ellipsoidal or fusiform proximal cells and usually 1-2 ellipsoidal or spherical distal cells forming a crown around the carpogonia; carpogonia 37–72 µm long, with sessile and club- or pear-shaped trichogynes; fertilized carpogonia and subtending cells of carpogonial branches with enlarged pit-connections; carposporophytes pedicellate, spherical or sub-spherical, contained within the whorls, 1-3(-5) per whorl, small, 67-211 μm in diameter; gonimoblast filaments densely arranged, composed of 1–3 cylindrical or barrel-shaped cells; carposporangia obovoid or pear-shaped, 24-42 μm long, 16-30 μm wide.

Distribution: North America (USA) (Sheath *et al*. 1994, this study); the species is primarily recorded from the coastal plain in the Southeastern US.

Additional specimens examined: USA: Alabama, Mississippi (Table S1).

Representative DNA sequences: EU636755, EU636759, KT802766 (COI-5P); AF029145, EU106052, EU106055 (*rbc*L).

Remarks: Collins (1906) proposed the name *Batrachospermum australe* in a footnote for specimens distributed in the Phycotheca Boreali-Americana (as 1087). *Batrachospermum macrosporum* as he noted was not available due to Montagne's earlier use of the species epithet. Sheath *et al*. (1994) designated the herbarium sheet at MICH as a lectotype. Specimens at MICH have been digitized and specimen #642701 was annotated by Sheath and is assumed to be the lectotype. Previous records of 'Chantransia macrospora' (also as *Audouinella macrospora*) and *Batrachospermum macrosporum* from North America most likely represent this species, especially those reports from the southeastern coastal plain and as far north as New Jersey Pine Barrens.

There were two notable morphological observations. Carpogonial branches with secondary carpogonial branches as involucral filaments was observed in at least one population (NC). This characteristic has been observed in other genera particularly *Sheathia*.

In two populations (NC and AL01) the carpospores were seen to be germinating immediately after release from the carposporangium and started to produce chantransia filaments on the gametophyte thallus. This observation has also been made in *M. macrospora* from Brazil, but to our knowledge has not been documented in other Batrachospermales genera.

SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://

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FIGURE LEGENDS

Fig. 1. Maximum-likelihood phylogeny showing relationship of *Montagnia* gen. nov. with sections of *Batrachospermum* and other genera of Batrachospermales based on *rbc*L sequence data. * = bootstrap support > 90 and posterior probability > 0.90; nodes without values indicate bootstrap values < 70 and posterior probability < 0.90. Information on the sequences are listed in Table S1 (Supporting Information). Scale represents substitutions per site. Newly generated sequences are in boldface.

Fig. 2. Phylogenetic tree (maximum likelihood) showing relationship among specimens of *Montagnia* based on concatenated *rbc*L and COI-5P sequence data. * = bootstrap support > 90 and posterior probability > 0.90; nodes without values indicate bootstrap values < 70 and posterior probability < 0.90. Information on the sequences are listed in Table S1 (Supporting Information). Scale represents substitutions per site. Newly generated sequences are in boldface.

Figs 3-14. Photomicrographs showing key morphological characters of *Montagnia macrospora* comb. nov. Herbarium specimen codes as in Table S1.

Figs 3-4. Barrel-shaped whorls showing pedunculate carposporophyte (arrow) (SJRP 31481) and monosporangia (arrowheads) (SJRP 31489). Scale bars = 500 µm.

Fig. 5. Primary fascicle composed of elongate cylindrical cells that become ovoid near the fascicle tip (SJRP 31481). Scale bar = 100 µm.

Fig. 6. Pear-shaped monosporangia at the tips of fascicles (SJRP 31489). Scale bar = 50 µm.

Fig. 7. Young carpogonium with club-shaped trichogyne (arrow) on a > 6-celled carpogonial branch with one-celled involucral branches (SJRP 31487). Scale bar = 25 µm. **Fig. 8.** Mature carpogonium showing ovoid trichogyne (arrow) and upper involucral cell (arrowhead) forming a crown around carpogonium (SJRP 31488). Scale bar = 10 µm.

Fig. 9. Carpogonial branch showing enlarged pit connection (arrows) between barrel-shaped cells (SJRP 31488). Scale bar = 10 µm.

Fig. 10. Carposporophyte with large obovoid and pear-shaped carposporangia (arrows) (SJRP 31488). Scale bar = 25 µm.

Figs 11-14. Post-fertilization stages (SJRP 31487). Scale bars = 25 µm. **Fig. 11.** Fertilized carpogonium showing a club-shaped trichogyne (arrow) with attached spermatium (arrowhead), upper involucral cells (double arrowheads) forming a crown around carpogonium and carpogonial branch with enlarged pit connection between cells (white arrow). **Fig. 12.** Carpogonial branch showing enlarged pit connections (arrows) between cells. **Fig. 13.** Developing carposporophyte showing large carposporangia (arrowheads) and carpogonial branch with enlarged pit connection between cells (arrows). **Fig. 14.** Carpogonial branch showing enlarged pit connection (arrow).

Figs 15-22. Photomicrographs showing key morphological characters of *Montagnia australis* comb. nov. Herbarium specimen codes as in Table S1.

Fig. 15. Obconic whorls with abundant secondary fascicles showing pedunculate carposporophyte (arrow) (BHO A-0143). Scale bar = 500 µm.

Fig. 16. Barrel-shaped whorls showing pedunculate carposporophytes (arrows) and chantransia filaments (arrowheads) from carpospores (double arrowheads) that have germinated on the gametophyte thallus (BHO A-1568). Scale bar = 500 µm.

Fig. 17. Primary fascicle composed of elongate cylindrical cells that become obovoidal near the fascicle tip (BHO A-1565). Scale bar = 50 µm.

Fig. 18. Spherical spermatangia (arrows) at the tips of fascicles (BHO A-1568). Scale bar = 20 µm.

Figs 19-20. Carpogonia on straight multi-celled branches. **Fig. 19.** Carpogonium with an elongate club-shaped trichogyne (arrow) on a 5-celled carpogonial branch with upper involucral cells (arrowheads) forming a crown around carpogonium (BHO A-1565). Scale bar = 30 µm. **Fig. 20.** Carpogonium with a pear-shaped trichogyne (arrow) on a carpogonial branch with upper involucral cells (arrowheads) forming a crown around carpogonium (BHO A-1564). Scale bar = 30 µm.

Fig. 21. A carpogonial branch with enlarged pit connections between cells (arrows) after the carposporophyte has developed (BHO A-1564). Scale bar = 20 µm.

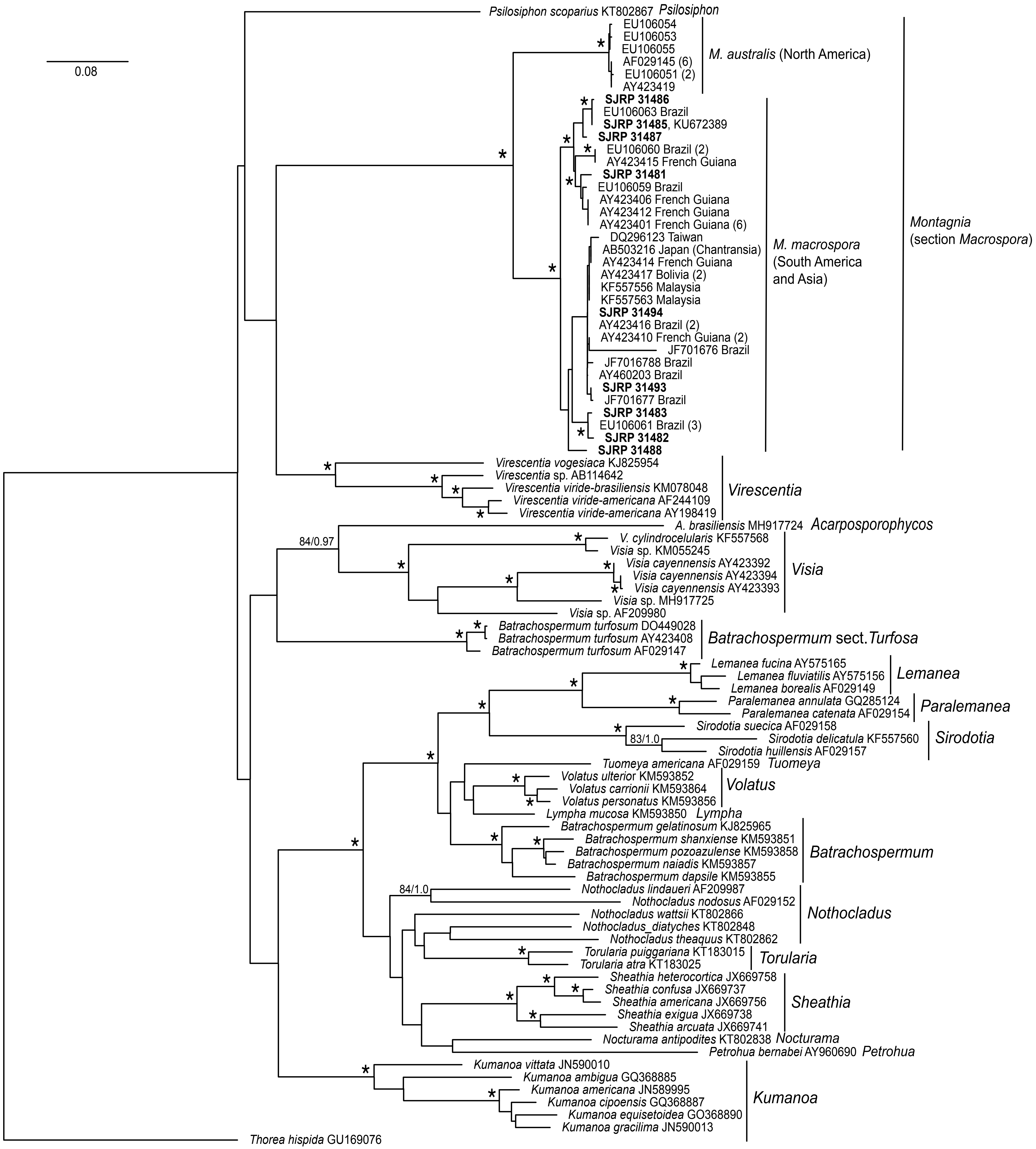
Fig. 22. Carposporophyte with large obovoid and pear-shaped carposporangia (arrows) (BHO A-1564). Scale bar = 30 µm.

FIGURE LEGENDS – SUPPLEMENTARY

Figure S1. Graphical results of ABGD analysis for *rbc*L sequences of specimens of section *Macrospora*: a. Histogram of distances; b. Ranked distances. Sequences used in the analysis are listed in Table S2.

Fig. S2. Distance tree (Neighbor joining) showing relationship among specimens of *Montagnia* based on COI-5P sequence data. * = bootstrap support > 90 and posterior probability > 0.90; nodes without values indicate bootstrap values < 70 and posterior probability < 0.90. Information on the sequences are listed in Table S1 (Supporting Information). Scale represents substitutions per site. Newly generated sequences are in boldface.

Figure S3. Graphical results of ABGD analysis for COI-5P sequences of specimens of section *Macrospora*: a. Histogram of distances; b. Ranked distances. Sequences used in the analysis are listed in Table S2.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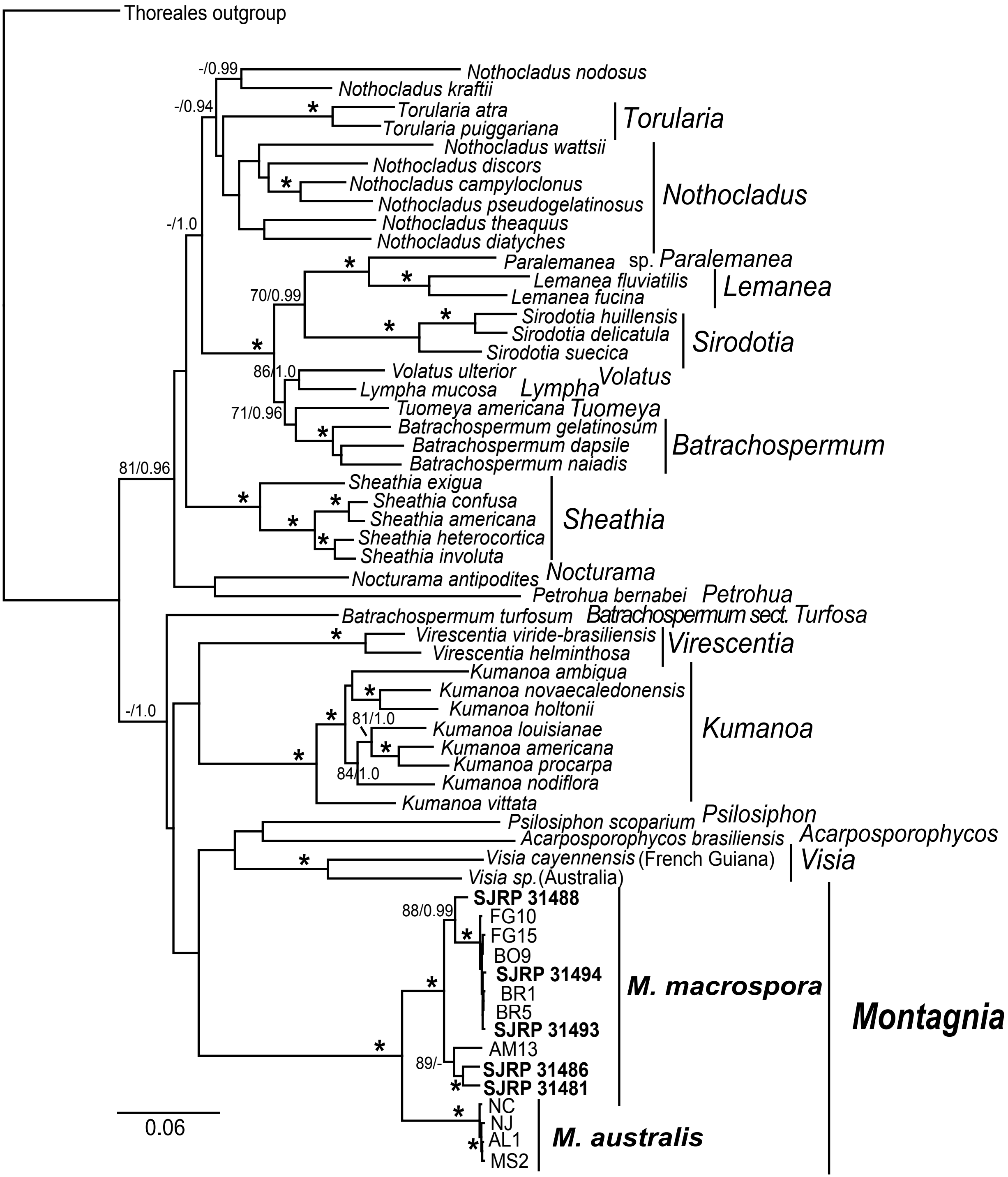
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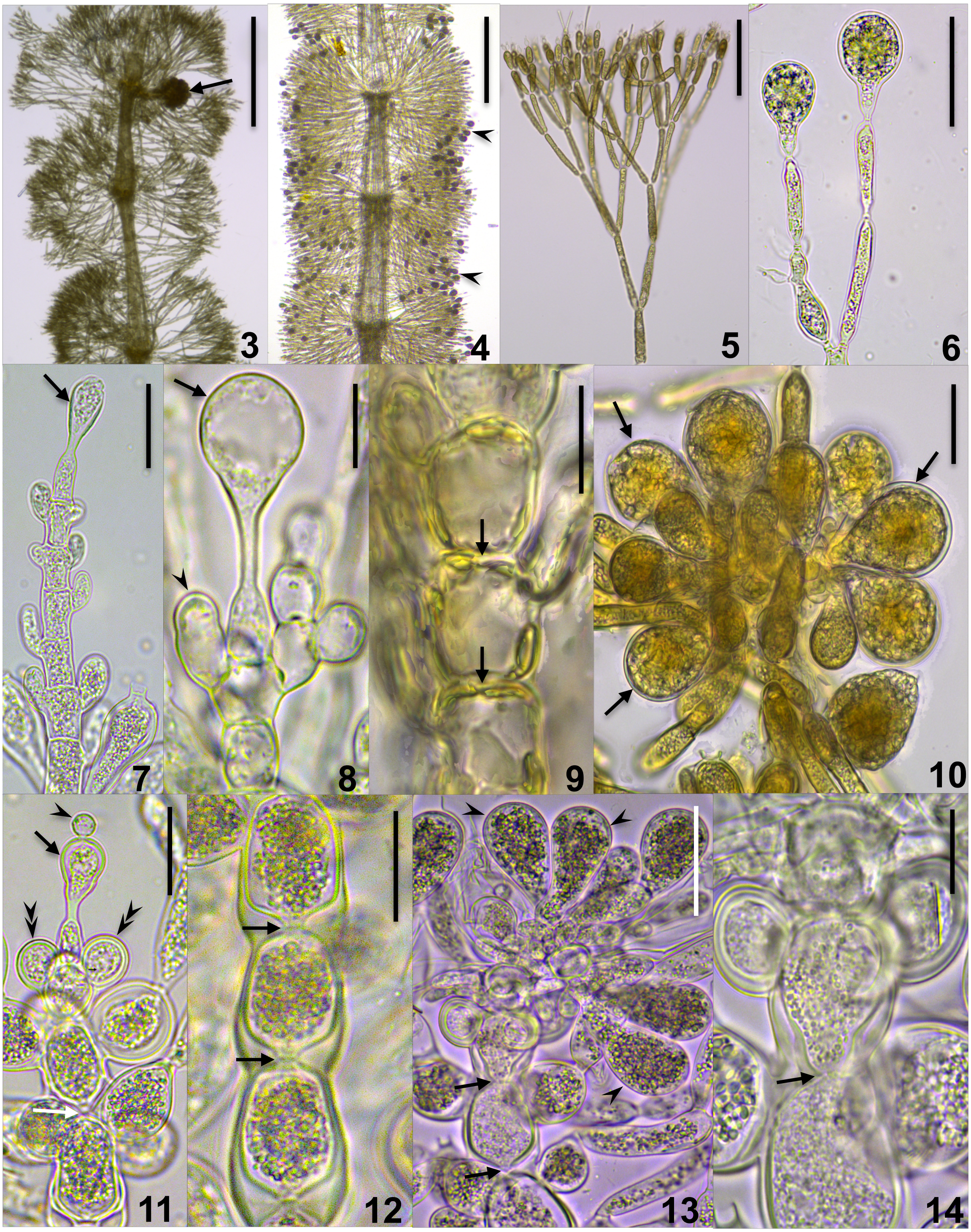
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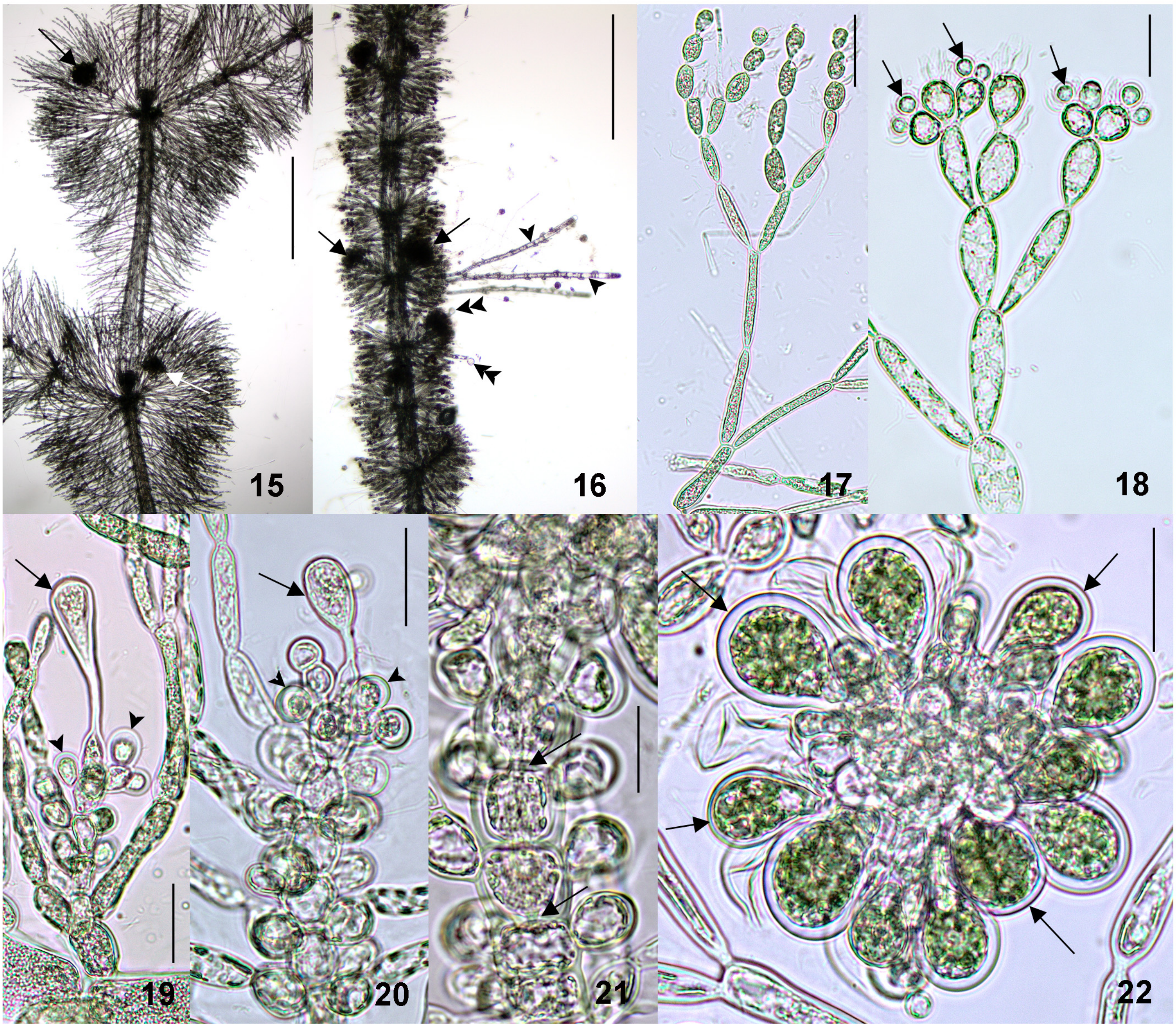
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