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Ingoldian fungi of Brazil: some new records and a review including a checklist and a key

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Abstract

Ingoldian fungi have a worldwide distribution, but the most species have been described from temperate regions. In Brazil, the studies of Ingoldian fungi started in the 1980's in the Atlantic Forest, the state of São Paulo. Later studies extended to other biomes such as the Cerrado, Caatinga and Amazon. The aim of this study is to improve our understanding of the occurrence and distribution of Ingoldian fungi in Brazil. Here, we include and discuss several new records for Brazil associated with submerged leaves of *Calophyllum brasiliense* and provide a checklist, a key and illustrations for all species of the Ingoldian fungi recorded from Brazil, as well as distribution maps. *Flagellospora stricta* is a new record to the Americas; *Dendrosporomyces prolifer* and *Geniculospora inflata* to the Neotropics; *Pyramidospora casuarinae* and *Triscelophorus monosporus* are new records to the Caatinga. With the new additions of species associated with submerged leaves of *C. brasiliense,* a total of 85 taxa of Ingoldian fungi are now recorded in Brazil. Nineteen taxa are reported from the Amazon, 53 from the Atlantic Forest, 39 from the Caatinga and 21 from the Cerrado.

Key-words: aquatic hyphomycetes, biodiversity, tropical

Introduction

Ingoldian fungi are asexual stages of ascomycetes or basidiomycetes (Shearer *et al.* 2007) adapted to aquatic environments. They are identified mainly based on the morphological features of conidia that are often quite unique: branched, sigmoid, tetraradiate, or multiradiate. Earlier studies based on anamorph-teleomorph connections (Webster 1992) and more recent molecular data (Belliveau & Bärlocher 2005, Baschien *et al.* 2006) have shown that Ingoldian fungi are polyphyletic. The majority of species analyzed have affinity with the Leotiomycetes (Helotiales), while some species are closely related to Dothideomycetes (Dothideales and Pleosporales), Orbiliomycetes (Orbiliales) or Sordariomycetes (Hypocreales) (Belliveau & Bärlocher 2005, Baschien *et al.* 2006, 2013, Campbell *et al.* 2009, Shearer *et al.* 2014); very few species are of basidiomycetous affinity. Ingoldian fungi have worldwide distribution (Jones & Pang 2012) but the highest number of species has been described from temperate regions (Silva & Briedis 2011).

Aquatic fungi are essential in the decomposition of submerged plant litter and are the key players in aquatic ecosystems facilitating the transfer of energy and nutrients to higher tropic levels (Gessner *et al.* 2007). Ingoldian fungi demonstrate the production of a wide variety of enzymes with cellulolytic, pectinolytic and proteolytic activity (Shearer 1992). Some of these fungi have been also reported to produce antimicrobial secondary metabolites (Gulis & Stephanovich 1999, Arya & Sati 2011).

De Wildeman described three genera of Ingoldian fungi in the 1890: *Clavariopsis* De Wild. (1895: 200), *Lemonniera* De Wild. (1894: 147) and *Tetracladium* De Wild. (1893: 39) (De Wildeman 1893, 1894, 1895). The group received more attention in 1942, with the Ingold's study that named the group "aquatic hyphomycetes" and listed 16 species, seven new genera, 11 new species and two new combinations (Ingold 1942). C.T. Ingold collected and published extensively on the Ingoldian fungi from temperate and tropical regions and inspired more interest in this group (Ingold 1949, 1958a, 1959, Hudson & Ingold 1960).

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Nilsson (1962a) began the studies of Ingoldian fungi in South America collecting from rivers in Venezuela and described two new genera: *Angulospora* Sv. Nilsson (1962: 354) and *Pyramidospora* Sv. Nilsson (1962: 358). Later reports came from Argentina, Brazil, Chile, Colombia, Ecuador, Peru and Venezuela (Gamundi *et al.* 1977, Burgos & Riffart 1982, Schoenlein-Crusius & Milanez 1989, Matsushima 1993, Luna-Fontalvo 2009, Silva & Briedis 2016). Matsushima (1993) described a new species, *Triscelophorus curviramifer* Matsush. (1993: 70) and proposed a new combination *T. deficiens* (Matsush.) Matsush. (1993: 70) from Peru.

In Brazil, the studies of Ingoldian fungi started in the 1980's on submerged leaves of *Ficus microcarpa* L.f. (1782: 442) in the Atlantic Forest, the state of São Paulo (Schoenlein-Crusius & Milanez 1989). Later studies extended to other biomes such as the Cerrado, Caatinga and Amazon (Schoenlein-Crusius 2002, Fiuza & Gusmão 2013a, Fiuza *et al.* 2015). Schoenlein-Crusius & Grandi (2003) reviewed the diversity of aquatic hyphomycetes in South America and reported 31 taxa of Ingoldian fungi from Brazil.

The aim of this study is to improve our understanding of the occurrence and distribution of Ingoldian fungi in Brazil. Here, we include and discuss several new records for Brazil associated with submerged leaves of *Calophyllum brasiliense* Cambess. in Saint-Hilaire (1825: 320) and provide a checklist, a key and illustrations for all species of the Ingoldian fungi recorded from Brazil, as well as distribution maps.

Materials and Methods

Study area

From November 2013 to January 2015, we made eight expeditions to "Serra da Tromba", located in the Chapada Diamantina, a semiarid region in northeastern Brazil. Submerged leaves of *C. brasiliense* were collected from three streams in the Contas river basin after several weeks of decomposition in litter bags. The samples were taken to the Laboratory of Mycology (LAMIC) in plastic bags, and processed according to Castañeda Ruiz *et al.* (2016) and Bärlocher (2005).

Sampling methods

Castañeda Ruiz *et al.* (2016): The samples were washed and placed in Petri dishes (moist chambers) incubated in a polystyrene box with sterile water plus glycerol for 30 days. Fungal structures were mounted on slides with lactic acid and sealed with nail polish. Some fungi were also isolated into pure culture.

Bärlocher (2005): Leaf samples were washed and 12-mm diam discs cut with a cork borer. The discs were incubated for 48 hours at 18–20ºC on a shaker (100rpm) in 100-mL Erlenmeyer flasks containing 30 mL of sterile distilled water to induce sporulation. The spore suspensions were filtered through membrane filters (5 µm pore size), and the filters were then mounted on slides with cotton blue in lactic acid. The leaf discs were also mounted on slides and examined under compound microscope. The specimens are deposited in the Herbarium of "Universidade Estadual de Feira de Santana" (HUEFS).

Venn diagram showing the distribution of Ingoldian fungi among different biomes was made using software available at Bioinformatics & Evolutionary Genomics (2016) site.

Results

In the present study in the Caatinga, we found 15 taxa of Ingoldian fungi from 12 genera (Table 1) associated with submerged leaves of *Calophyllum brasiliense*. *Flagellospora stricta* Sv. Nilsson (1962b:82) is a new record to the Americas; *Dendrosporomyces prolifer* Nawawi, J. Webster & R.A. Davey (1977: 59) and *Geniculospora inflata* (Ingold) Sv. Nilsson ex Marvanová & Sv. Nilsson (1971: 532) to the Neotropics; *Pyramidospora casuarinae* Sv. Nilsson (1962a: 359) and *Triscelophorus monosporus* Ingold (1943: 152) are new records to the Caatinga. All new records are discussed in details in the Taxonomy section below.

With these additions, a total of 85 taxa of Ingoldian fungi are now reported from Brazil (Table 2). Of those, 19 taxa are known from the Amazon, 53 from the Atlantic Forest, 39 from the Caatinga and 21 from the Cerrado (Fig. 1). All species of Ingoldian fungi that has been found in Brazil are illustrated in Figs. 2–7. In addition, a key to all taxa and maps showing study sites and distribution are provided (Figs. 8–9).

TABLE 1. Taxa of Ingoldian fungi associated with *Calophyllum brasiliense* in this study.

Taxa	Moist chambers (after Castañeda-Ruiz *et al.* 2016)	Submerged incubations (after Bärlocher 2005)
Anguillospora filiformis **Greath.**		x
A. longissima **(Sacc. & P. Syd.) Ingold**		x
Condylospora gigantea **Nawawi & Kuthub.**		x
Dendrosporium lobatum **Plakidas & Edgerton ex J.L. Crane**	x	x
Dendrosporomyces prolifer **Nawawi, J. Webster & R.A. Davey**	x	x
Filosporella **sp.**	x	x
Flagellospora curvula **Ingold**		x
F. stricta **Sv. Nilsson**		x
Geniculospora inflata **(Ingold) Sv. Nilsson ex Marvanová & Sv. Nilsson**	x	
Ingoldiella hamata **D.E. Shaw**	x	
Lunulospora curvula **Ingold**		x
Pyramidospora casuarinae **Sv. Nilsson**		x
Scutisporus brunneus **K. Ando & Tubaki**		x
Triscelophorus acuminatus **Nawawi**	x	x
T. monosporus **Ingold**		x

TABLE 2. Taxa of Ingoldian fungi recorded from Brazil.

Taxa	Substrate	Biome	Reference	Ilustration from
Alatospora acuminata **Ingold**	Submerged leaf litter	Atlantic Forest	Malosso (1999)	Ingold (1942); Fiuza & Gusmão (2013a); Fiuza *et al.* (2015)
	Foam	Caatinga	Fiuza & Gusmão (2013a)	
	Foam	Amazon	Fiuza *et al.* (2015)	
Anguillospora crassa **Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a , 1990b), Schoenlein-Crusius *et al.* (2009, 2014, 2015a, 2015b, 2016)	Ingold (1958b)
	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg.	Atlantic Forest	Schoenlein-Crusius & Milanez (1998a, 1998b)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn	Atlantic Forest	Moreira (2006), Schoenlein-Crusius *et al.* (2015b, 2016)	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
	Submerged leaves of *Caesalpinia echinata* Lam.	Atlantic Forest	Moreira (2011), Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaf litter	Cerrado	Malosso (1999), Schoenlein-Crusius (2002)	
A. filiformis **Greath.**	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	Present study
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009)	
	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
A. furtiva **J. Webster & Descals**	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	Descals *et al.* (1998)
A. longissima **(Sacc. & P. Syd.) Ingold**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Present study
	Submerged leaf litter	Amazon	Fiuza *et al.* (2015)	
	Submerged leaf litter	Cerrado	Malosso (1999), Schoenlein-Crusius (2002)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
A. longissima **(Sacc. & P. Syd.) Ingold**	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2009), Schoenlein-Crusius *et al.* (2014, 2015a, 2015b)	
	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011), Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	
	Submerged leaf litter of *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius & Milanez (1989, 1990a, b), Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves of *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1992)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
Anguillospora **sp.**	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg., *Ficus microcarpa* L. f. and *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1992)	
	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2014, 2015b)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Moreira (2006)	
	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011)	
Aquanectria penicillioides **(Ingold) L. Lombard & Crous**	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	Ingold (1944)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015a, 2015b)	
A. submersa **(H.J. Huds.) L. Lombard & Crous**	Submerged leaf litter	Cerrado	Malosso (1999)	Hudson (1961)
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
Articulospora tetracladia **Ingold**	Submerged leaf litter	Atlantic Forest	Malosso (1999)	Ingold (1942); Fiuza & Gusmão (2013a)
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
	Foam	Caatinga	Fiuza & Gusmão (2013a)	
	Foam	Amazon	Fiuza *et al.* (2015)	
Articulospora **sp.**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009)	
Brachiosphaera tropicalis **Nawawi**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Descals *et al.* (1976); Fiuza & Gusmão (2013a)
	Submerged bark	Caatinga	Barbosa *et al.* (2013)	
	Submerged leaf litter	Amazon	Monteiro (2014)	
Campylospora brasiliensis **L. B. Moro & Schoenl.-Crus.**	Submerged leaf litter	Atlantic Forest	Moro *et al.* (2015)	Moro *et al.* (2015)

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
***C. chaetocladia* Ranzoni**	Foam	Caatinga	Fiuza & Gusmão (2013b)	Fiuza & Gusmão (2013b); Ranzoni (1953)
	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015b, 2016)	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
***C. filicladia* Nawawi**	Foam	Caatinga	Fiuza & Gusmão (2013b)	Fiuza & Gusmão (2013b)
***C. parvula* Kuzuha**	Foam	Caatinga	Fiuza & Gusmão (2013b)	Fiuza & Gusmão (2013b)
	Submerged leaf litter	Cerrado	Malosso (1999)	
***Campylospora* sp.**	Foam	Caatinga	Fiuza & Gusmão (2013b)	
***Clavariopsis aquatica* De Wild.**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a and 1990b)	De Wildeman (1895)
	Submerged leaf litter	Cerrado	Malosso (1999)	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
***Condylospora flexuosa* Nawawi & Kuthub.**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
***C. gigantea* Nawawi & Kuthub.**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Present study
	Foam	Amazon	Fiuza *et al.* (2015)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
***C. spumigena* Nawawi**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
***Condylospora* sp.**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
	Foam	Amazon	Fiuza *et al.* (2015)	
***Culicidospora aquatica* R.H. Petersen**	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	Petersen (1960)
***C. gravida* R.H. Petersen**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
***Dactylella microaquatica* Tubaki**	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2015b)	Tubaki (1957)
	Submerged leaf litter	Cerrado	Malosso (1999)	
***Dendrospora erecta* Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2015b)	Ingold (1943)
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***Dendrospora* sp.**	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg. and *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius *et al.* (1992)	
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2014)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
Dendrosporium lobatum **Plakidas & Edgerton ex J.L. Crane**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza & Gusmão (2013a); Fiuza *et al.* (2015)
	Soil	Atlantic Forest	Cavalcanti & Milanez (2007)	
	Submerged leaf litter	Caatinga	Fiuza & Gusmão (2013a)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
Dendrosporomyces prolifer **Nawawi, J. Webster & R.A. Davey**	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	Present study
D. splendens **(Nawawi) Nawawi & J. Webster**	Leaves of *Alchornea triplinervia* (Spreng.)Mull. Arg.	Atlantic Forest	Grandi (1998)	Nawawi (1973)
	Leaves of *Euterpe edulis* Mart.	Atlantic Forest	Grandi (1999)	
Dwayaangam **sp. as** ***Dwayaangam cornuta*** **in Fiuza et al. (2015)**	Foam	Amazon	Fiuza *et al.* (2015)	
Filosporella versimorpha **Marvanová, P.J. Fisher, Aimer & B.C. Segedin as** ***Anguillospora pseudolongissima*** **in Fiuza & Gusmão (2013a)**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Ranzoni (1953), Fiuza & Gusmão (2013a)
Filosporella **sp.**	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
Flabellocladia tetracladia **(Nawawi) Nawawi**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
Flabellospora crassa **Alas.**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a and 1990b), Schoenlein-Crusius *et al.* (2009, 2015a, 2015b)	Alasoadura (1968a)
	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	
F. multiradiata **Nawawi**	Submerged leaf litter	Amazon	Monteiro (2014)	Monteiro (2014)
F. verticillata **Alas.**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
Flagellospora curvula **Ingold**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Present study
	Foam	Amazon	Fiuza *et al.* (2015)	
	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2009, 2015a, 2015b	
	Submerged leaf litter	Cerrado	Malosso (1999)	
	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
Flagellospora **sp.**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2014, 2016)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Illustration from
F. stricta **Sv. Nilsson**	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	Present study
Geniculospora inflata **(Ingold) Sv. Nilsson ex Marvanová & Sv. Nilsson**	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	Present study
Heliscella stellata **(Ingold & Cox) Marvanová**	Submerged leaf litter	Cerrado	Malosso (1999)	Ingold & Cox (1957)
Heliscus **sp.**	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Moreira (2006)	
Ingoldiella hamata **D.E. Shaw**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
	Submerged bark and petiole	Caatinga	Barbosa *et al.* (2013)	
	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	
	Submerged leaf litter	Amazon	Monteiro (2014)	
	Submerged leaf litter	Caatinga	Silva *et al.* (2014)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
Isthmotricladia **sp.**	Submerged leaves of *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1990)	
Jaculispora submersa **H.J. Huds. & Ingold**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
Lemonniera alabamensis **R.C. Sinclair & Morgan-Jones**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
L. aquatica **De Wild.**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2009, 2015b)	
	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	
	Submerged leaves of *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius & Milanez (1989, 1990a)	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
	Submerged leaves of *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1990, 1992)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
L. pseudofloscula **Dyko**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
Lemonniera **sp.**	Submerged leaf litter	Cerrado	Attili & Tauk-Tornisiello (1994)	
Lunulospora curvula **Ingold**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
	Submerged leaf litter	Cerrado	Malosso (1999), Schoenlein-Crusius (2002)	
	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2009, 2014, 2015a, 2016)	
	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	
	Submerged leaf litter and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011), Schoenlein-Crusius *et al.* (2015b)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Illustration from
***Lunulospora curvula* Ingold**	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg., *Ficus microcarpa* L. f., *Quercus robur* L. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a, 1990b, 1998b)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***L. cymbiformis* Miura**	Submerged leaf litter	Cerrado	Malosso (1999), Schoenlein-Crusius (2002)	Marvanová (1997)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2015a, 2015b)	
***Lunulospora* sp.**	Submerged leaves of *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius & Milanez (1989)	
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015a)	
***Margaritispora aquatica* Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2014, 2015a, 2015b)	Ingold (1942)
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***Margaritispora* sp.**	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg., *Ficus microcarpa* L. f. and *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1992)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***Mycocentrospora acerina* (R. Hartig) Deighton**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009)	Gulis *et al.* (2005)
	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	
	Submerged leaf litter	Cerrado	Malosso (1999)	
***Mycofalcella calcarata* Marvanová, Om-Kalth. & J. Webster**	Submerged leaf litter	Caatinga	Sales *et al.* (2014)	Marvanová *et al.* (1993)
***Naiadella fluitans* Marvanová & Bandoni**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015b)	Marvanová & Bandoni (1987)
***Pyramidospora casuarinae* Sv. Nilsson**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009)	Present study
	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011), Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
***P. densa* Alas.**	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011)	Alasoadura (1968b)
***P. quadricelullaris* M.S. Oliveira, Malosso & R.F. Castañeda**	Submerged leaf litter	Atlantic Forest	Oliveira *et al.* 2015	Oliveira *et al.* (2015)
***P. robusta* Moreira & Schoenlein-Crusius**	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira & Schoenlein-Crusius (2012)	Moreira & Schoenlein-Crusius (2012)
***Pyramidospora* sp.**	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
***Pyramidospora* sp.**	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***Scutisporus brunneus* K. Ando & Tubaki**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Present study
	Foam	Amazon	Fiuza *et al.* (2015)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged petiole	Caatinga	Barbosa *et al.* (2013)	
***Tetrachaetum elegans* Ingold**	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	Ingold (1942)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2014, 2015b)	
	Submerged leaf litter and submerged leaves of *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg.	Atlantic Forest	Schoenlein-Crusius & Milanez (1998a, 1998b)	
	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg., *Ficus microcarpa* L. f., *Tibouchina pulchra* (Cham.) Cogn. and *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a and 1990b); Schoenlein-Crusius *et al.* (2016)	
***Tetracladium breve* A. Roldán**	Submerged leaf litter	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
***T. marchalianum* De Wild.**	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	Ingold (1942)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2014, 2015b)	
***T. maxiliiforme* (Rostr.) Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015b)	Ingold (1942)
***T. nainitalense* Sati & P. Arya**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
***T. setigerum* (Grove) Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2014, 2015b)	Ingold (1942)
***Tricladium angulatum* Ingold**	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	Ingold (1942)
***T. attenuatum* S.H. Iqbal as *T. fallax* in Fiuza & Gusmão (2013a)**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
***T. chaetocladium* Ingold**	Submerged leaves of *Protium heptaphyllum* Marchand and *Lafoensia pacari* A.St.-Hil.	Atlantic Forest	Rosa *et al.* (2009)	Ingold (1974)
***T. curvisporum* Descals**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
***T. gracile* Ingold**	Submerged leaf litter	Cerrado	Schoenlein-Crusius (2002)	Ingold (1944)
***T. splendens* Ingold**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009)	Ingold (1942)
***Trinacrium incurvum* Matsush.**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Fiuza & Gusmão (2013a)
***Triscelophorus acuminatus* Nawawi**	Foam	Caatinga	Fiuza & Gusmão (2013a)	Present study
	Foam	Amazon	Fiuza *et al.* (2015)	
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2014, 2015a)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
***Triscelophorus acuminatus* Nawawi**	Submerged leaf litter	Amazon	Monteiro (2014)	
	Submerged leaf litter and submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira & Schoenlein-Crusius (2012); Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves and bark	Caatinga	Silva *et al.* (2014)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***T. curviramifer* Matsush.**	Foam	Amazon	Fiuza *et al.* (2015)	Fiuza *et al.* (2015)
	Leaves of *Manilkara maxima* Penn. and *Parinari alvimii* Prance	Atlantic Forest	Magalhães *et al.* (2011)	
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***T. deficiens* (Matsush.) Matsush.**	Leaf litter	Caatinga	Cruz *et al.* (2007)	Fiuza *et al.* (2015)
	Leaves of *Manilkara maxima* Penn. e *Parinari alvimii* Prance	Atlantic Forest	Magalhães *et al.* (2011)	
	Foam	Amazon	Fiuza *et al.* (2015)	
***T. magnificus* Petersen**	Submerged leaves of *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius *et al.* (1990)	Petersen (1962)
	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2015b)	
***T. monosporus* Ingold**	Submerged leaf litter	Cerrado	Malosso (1999); Schoenlein-Crusius (2002)	Present study
	Submerged leaf litter	Atlantic Forest	Malosso (1999); Schoenlein-Crusius & Milanez (1990a ,1990b) Schoenlein-Crusius *et al.* (2014, 2015b)	
	Submerged leaf litter and submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011), Schoenlein-Crusius *et al.* (2015b)	
	Submerged leaves of *Quercus robur* L.	Atlantic Forest	Schoenlein-Crusius & Milanez (1990a , 1990b)	
	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg.	Atlantic Forest	Schoenlein-Crusius & Milanez (1998a, 1998b)	
	Submerged leaves of *Calophyllum brasiliense* Cambess	Caatinga	Present study	
	Submerged leaves of *Ficus microcarpa* L. f.	Atlantic Forest	Schoenlein-Crusius *et al.* (1990, 1992)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
***Triscelophorus* sp.**	Submerged leaf litter	Atlantic Forest	Malosso (1999), Schoenlein-Crusius *et al.* (2016)	
	Submerged leaf litter	Cerrado	Malosso (1999)	
	Submerged leaves of *Caesalpinia echinata* Lam. and *Campomanesia phaea* (O. Berg.) Landrum	Atlantic Forest	Moreira (2011)	
***Trisulcosporium acerinum* H.J. Huds. & B. Sutton**	Submerged leaves of *Alchornea triplinervia* Spreng. M. Arg.	Atlantic Forest	Schoenlein-Crusius *et al.* (1992)	Fiuza & Gusmão (2013a)
	Foam	Caatinga	Fiuza & Gusmão (2013a)	

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TABLE 2. (Continued)

Taxa	Substrate	Biome	Reference	Ilustration from
Varicosporium elodeae **W. Kegel**	Submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2009, 2015a)	Ingold (1942)
	Submerged leaf litter and submerged leaves of *Caesalpinia echinata* Lam.	Atlantic Forest	Moreira (2011), Schoenlein Crusius *et al.* (2015b)	
	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn. and submerged leaf litter	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	
Varicosporium **sp.**	Submerged leaves of *Tibouchina pulchra* (Cham.) Cogn.	Atlantic Forest	Schoenlein-Crusius *et al.* (2016)	

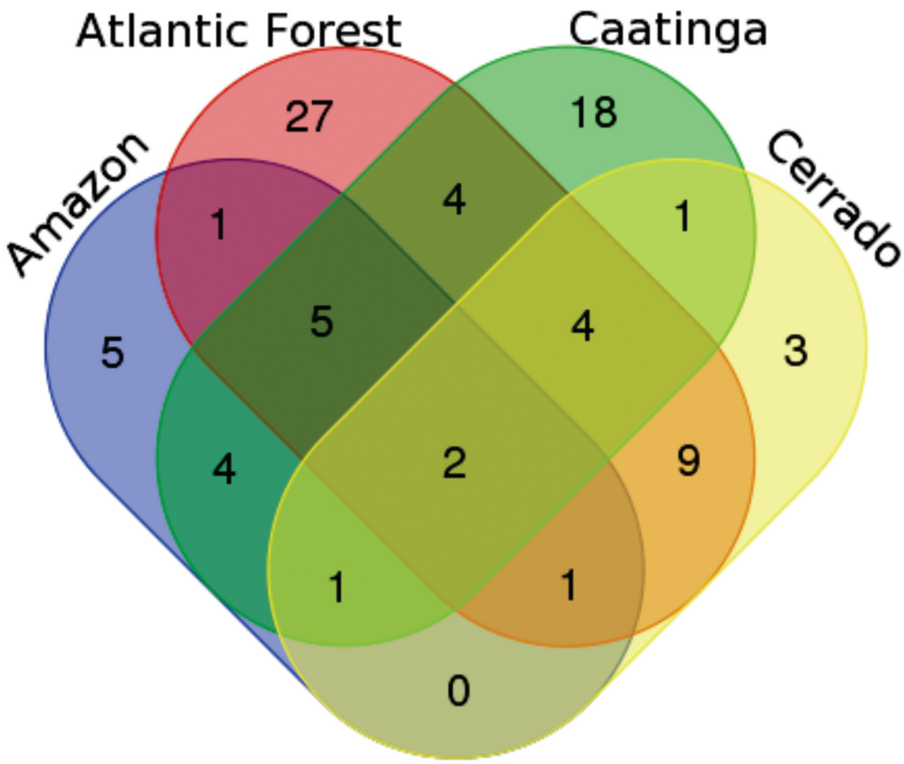

FIGURE 1. Venn diagram showing the number of Ingoldian taxa found in the different biomes in Brazil.

Taxonomy

Dendrosporomyces prolifer Nawawi, J. Webster & R.A. Davey, Trans. Br. mycol. Soc. 68: 59, 1977.
(Fig. 4A)

Material examined:—BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 10 November 2013, *P.O. Fiuza s.n* (HUEFS 215692); BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 07 September 2014, *P.O. Fiuza s.n* (HUEFS 215706).

Conidiophores not observed. Conidia hyaline, consisting of cylindrical, curved main axis with 7–10 primary branches. Main axis not constricted at septa, 14–20 septate, 150–440 × 7–10 µm; primary branches cylindrical, 4–17 septate, 198–335 × 8–10 µm, constricted at base, rounded at the apex; secondary branches cylindrical, 3–13 septate, 62–323 × 8–10 µm; branches constricted at base, rounded at the apex.

Geographical distribution:—India (Sridhar *et al.* 1992); Malaysia (Nawawi *et al.* 1977); USA (V. Gulis, unpublished).

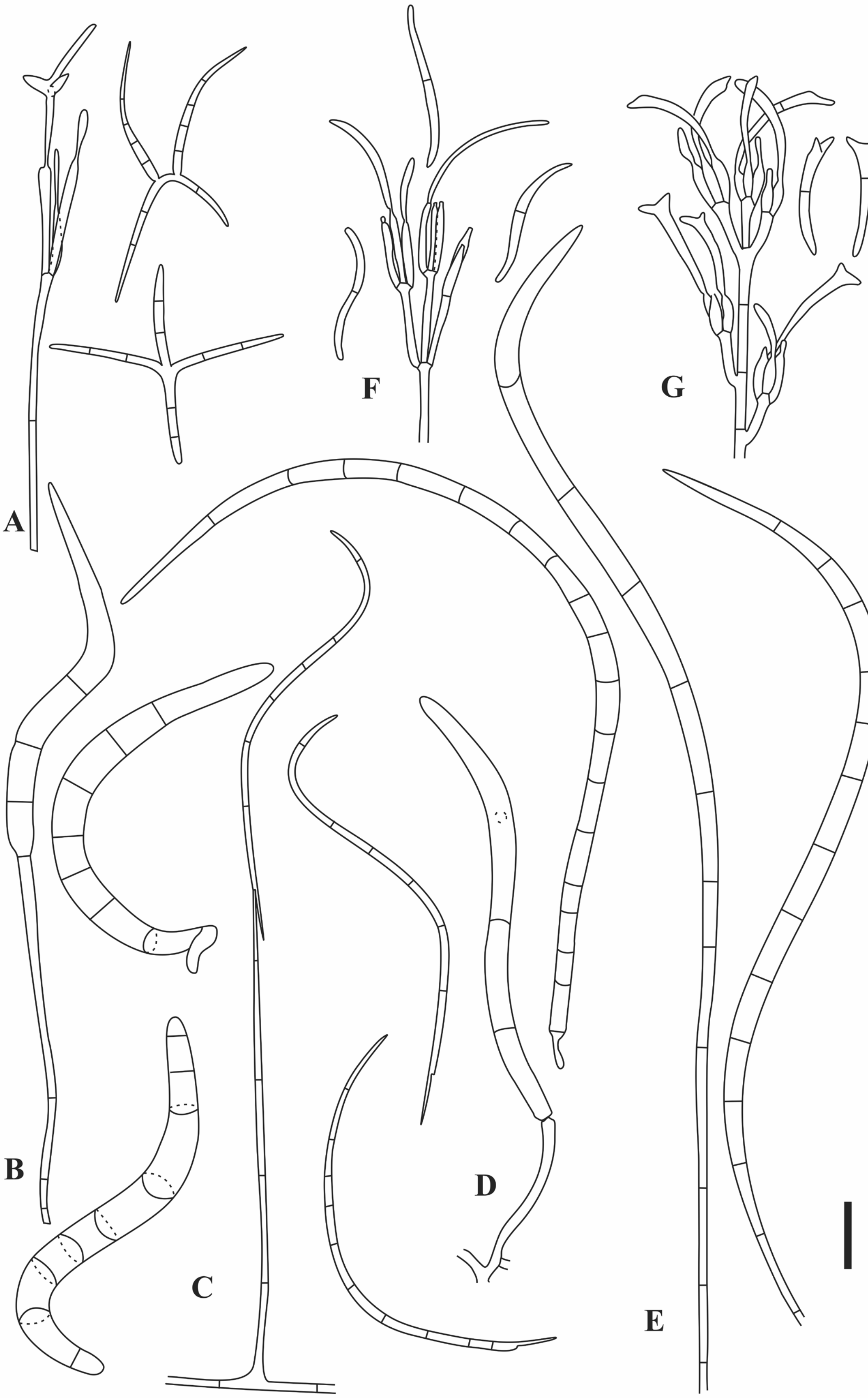

FIGURE 2. A. *Alatospora acuminata*: conidia and conidiophore; **B.** *Anguillospora crassa*: conidia and conidiophore; **C.** *Anguillospora filiformis*: conidia and conidiophore; **D.** *Anguillospora furtiva*: conidia and conidiophore; **E.** *Anguillospora longissima*: conidia and conidiophore; **F.** *Aquanectria penicillioides*: conidia and conidiophore; **G**. *Aquanectria submersa*: conidia and conidiophore. (Scale bar: A–B, D–G= 20 µm; C= 25 µm)

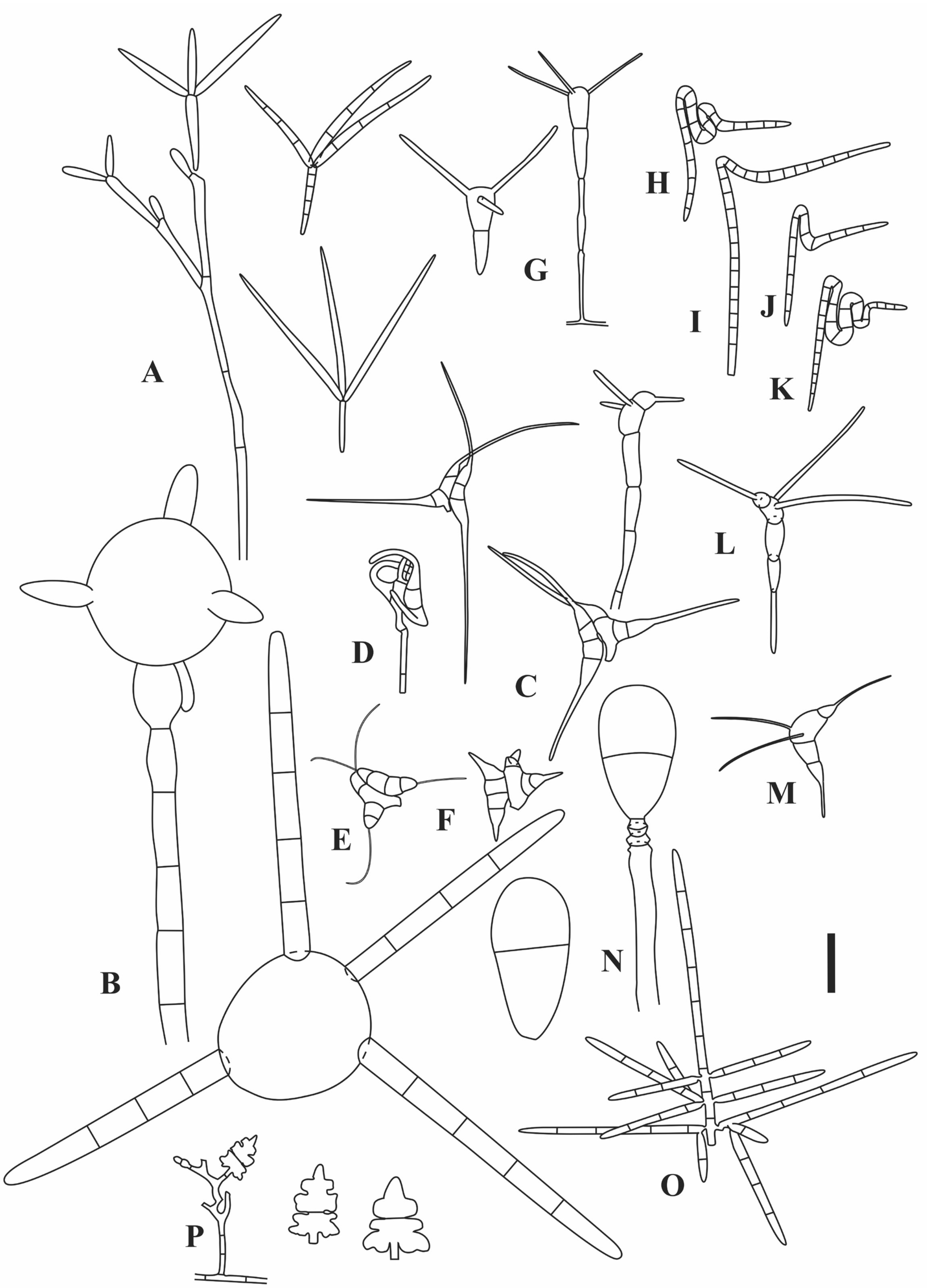

FIGURE 3. A. *Articulospora tetracladia*: conidia and conidiophore; **B.** *Brachiosphaera tropicalis:* conidia and conidiophore; **C.** *Campylospora brasiliensis:* conidium; **D.** *Campylospora chaetocladia:* conidia and conidiophore; **E.** *Campylospora filicladia*: conidium; **F.** *Campylospora parvula*: conidium; **G.** *Clavariopsis aquatica*: conidia and conidiophore; **H.** *Condylospora flexuosa*: conidium; **I.** *Condylospora gigantea*: conidium; **J.** *Condylospora spumigena*: conidium; **K.** *Condylospora* sp.; conidium; **L.** *Culicidospora aquatica*: conidia and conidiophore; **M.** *Culicidospora gravida:* conidium; **N.** *Dactylella microaquatica*: conidia and conidiophore; **O.** *Dendrospora erecta*: conidium; **P.** *Dendrosporium lobatum*: conidia and conidiophore. (Scale bar: A–B, H–M= 20 µm; C–F= 25 µm; G = 60 µm; N= 5 µm; O= 50 µm; P= 10 µm)

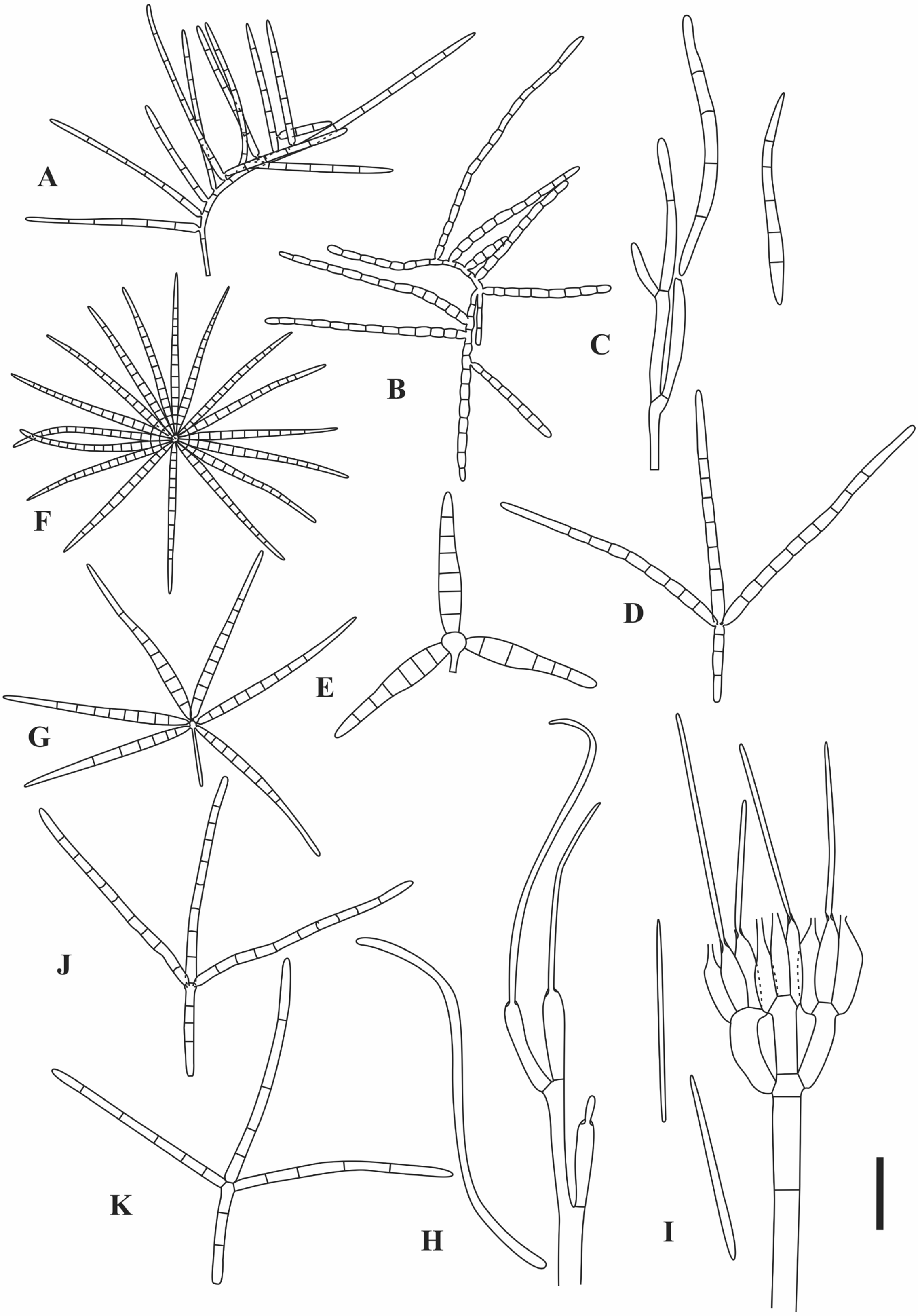

FIGURE 4. A. *Dendrosporomyces prolifer*: conidium; **B.** *Dendrosporomyces splendens*: conidium; **C.** *Filosporella versimorpha*: conidiophore and conidia; **D.** *Flabellocladia tetracladia*: conidium; **E.** *Flabellospora crassa*: conidium; **F.** *Flabellospora multiradiata*: conidium; **G.** *Flabellospora verticillata*: conidium; **H.** *Flagellospora curvula*: conidia, conidiophore and conidiogenous cells; **I.** *Flagellospora stricta*: conidia, conidiophore and conidiogenous cells; **J–K.** *Geniculospora inflata*: conidia. (Scale bar: A–B= 80 µm; C, E, G–H= 25 µm; D, J–K= 30 µm; F= 50 µm; I=10 µm)

Notes:—*Dendrosporomyces* is composed by two species: *D. prolifer* (type species) and *D. splendens* (Nawawi) Nawawi & J. Webster (Nawawi & Webster 1982). The genus is characterized by holoblastic, branched, hyaline conidia, consisting of a main axis bearing primary and secondary branches (Nawawi *et al.* 1977) and dolipore septa (Nawawi 1985a). *Dendrosporomyces prolifer* differs from *D. splendens* by having somewhat smaller, profusely branched conidia (Marvanová 1997). *Dendrosporomyces splendens* has been previously reported from Brazil on submerged leaves of *Euterpe edulis* Mart. (1824: 33) and *Alchornea triplinervia* (Spreng.) Mull. Arg. in Candolle (1866: 909) from the Atlantic Forest, the state of São Paulo (Grandi 1998, 1999). It is the first record of *D. prolifer* from Brazil.

Flagellospora stricta Sv. Nilsson, Bot. Notiser 115: 82, 1962. (Fig. 4I)

Material examined:—BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 10 November 2013, *P.O. Fiuza s.n* (HUEFS 215892).

Conidiophores branched, septate, hyaline, 40–60 × 4.5–5 µm. Conidiogenous cells phialidic, clavate, terminal, hyaline, 8–15 × 3–4.5µm. Conidia filiform, straight, aseptate, hyaline, 20–50 × 1–1.5 µm.

Geographical distribution:—Poland (Orłowska *et al.* 2004); Sweden (Nilsson 1962b, 1964).

Notes:—*Flagellospora stricta* is distinguished from other species of *Flagellospora* by having straight conidia (Nilsson 1962b). In Brazil, one species of *Flagellospora—F. curvula* (Ingold 1942: 404)—has been recorded from the Atlantic Forest on mixed submerged leaves (Schoenlein-Crusius *et al.* 2009), from the Caatinga in foam (Fiuza & Gusmão 2013a) and from the Amazon in foam (Fiuza *et al.* 2015). It is the first record of *Flagellospora stricta* for the Americas.

Geniculospora inflata (Ingold) Sv. Nilsson ex Marvanová & Sv. Nilsson, Trans. Br. mycol. Soc. 57: 532, 1971. (Figs. 4 J–K)

Material examined:—BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 18 December 2014, *P.O. Fiuza s.n* (HUEFS 215970).

Conidiophores simple, septate, hyaline, 40–45 × 3–5 µm. Conidia tetraradiate, hyaline, consisting of a cylindrical geniculate main axis and 2 lateral branches attached at the point of main axis inflection. Main axis 108–176 × 4.5–5 µm, somewhat inflated at the point of branch attachment, branches slightly constricted at base, 70–131 × 4.5–6 µm, elements septate.

Geographical distribution:—Austria (Marvanová & Gulis 2000); Canada (Sokolski *et al.* 2006); England (Ingold 1944); França (Fabre 1998); Greenland (Engblom *et al.* 1986); Hungary (Gönczöl & Révay 2011); India (Sridhar *et al.* 1992); Pakistan (Iqbal 1997); Portugal (Pascoal *et al.* 2005); Spain (Casado *et al.* 2015); USA (Suberkropp & Wallace 1992).

Notes:—*Geniculospora* is represented by two well known species: *G. grandis* Greath. ex Nolan (1972: 1173) and *G. inflata* (type species). *G. intermedia* (R.H. Petersen) Sv. Nilsson ex Marvanová & Sv. Nilsson (1971: 532) (Nolan 1972) is probably conspecific with *G. inflata*. The genus is characterized by hyaline, tetraradiate conidia with characteristically geniculate main axis, from the middle of which two other branches arise at the same level (Nilsson 1964). *Geniculospora grandis* displays nearly concurrent development of 3 elements, so the conidium can be interpreted as having 3 terminal arms originating from a relatively short stalk (main axis); conidia of *G. grandis* are also considerably larger than in *G. inflata* (Greathead 1961). *Geniculospora inflata* is a new record to the Neotropics.

Pyramidospora casuarinae Sv. Nilsson, Svensk bot. Tidskr. 56: 359, 1962. (Fig. 5M)

Material examined:—BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 10 November 2013, *P.O. Fiuza s.n* (HUEFS 216621).

Conidiophores simple, septate, hyaline 20–45 × 3–4.5 µm. Conidiogenous cells monophialidic, terminal, hyaline. Conidia multicellular (3–9 cells), with oblong cells arranged in a regular or irregular way, 3–4 cells each develop from the basal cell as well as from the top cell; conidia span 15–22 × 14–18 µm, each cell 5.3–7.5 × 4.5–6 µm.

Geographical distribution:—Brazil (Schoenlein-Crusius *et al.* 2009); Cuba (Marvanová & Marvan 1969); France (Jabiol *et al.* 2013); India (Sridhar & Kaveriappa 1992); Italy (Rodino *et al.* 2003); Pakistan (Bareen & Iqbal 1994); Poland (Czeczuga *et al.* 2007); Puerto Rico (Caballero 1983); Sweden (Nilsson 1964); Venezuela (Nilsson 1962a).

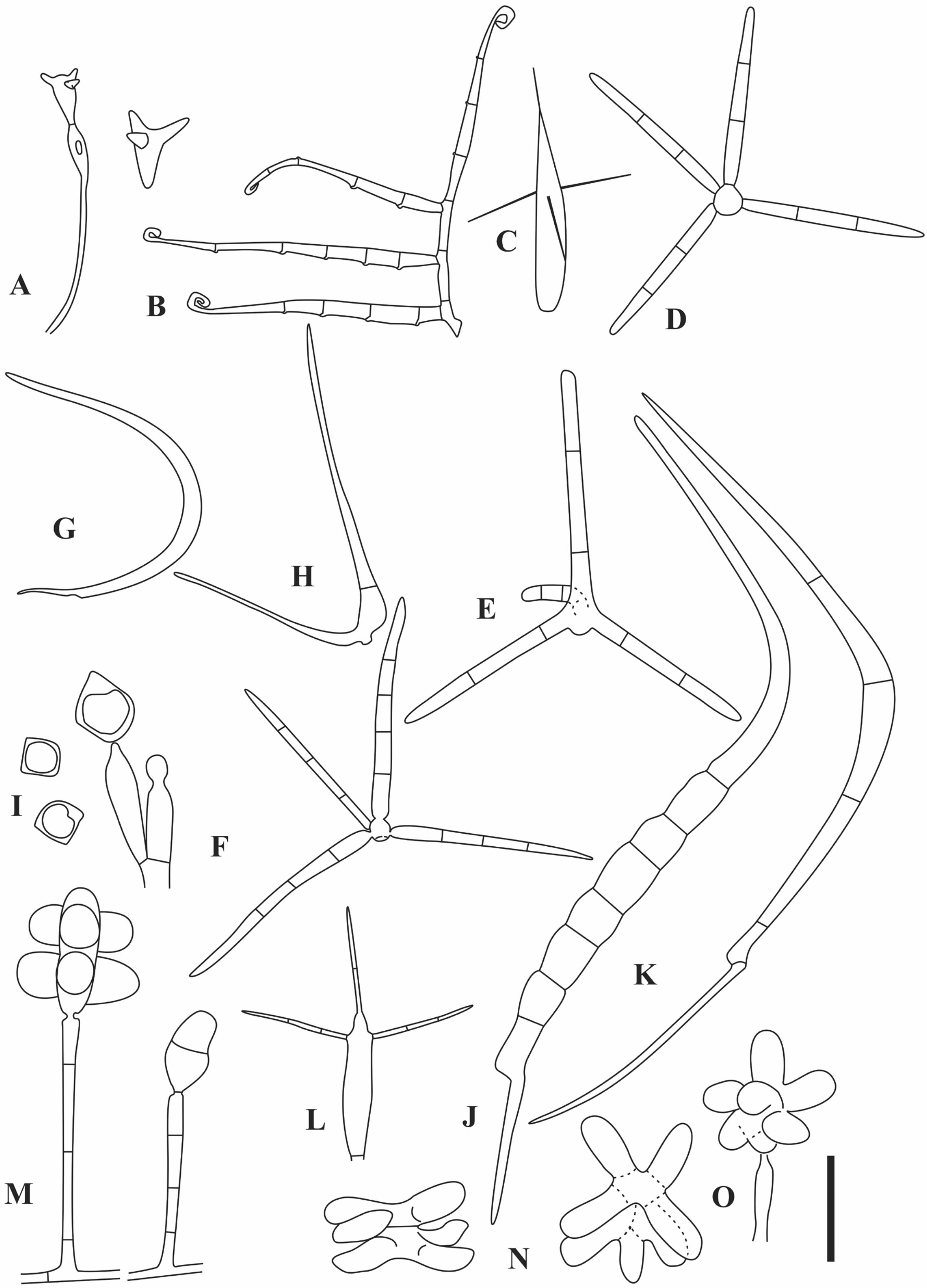

FIGURE 5. A. *Heliscella stellata*: conidia and conidiophore; **B.** *Ingoldiella hamata*: conidium; **C.** *Jaculispora submersa*: conidium; **D.** *Lemonniera alabamensis*: conidium; **E.** *Lemonniera aquatica*: conidium; **F.** *Lemonniera pseudofloscula*: conidium; **G.** *Lunulospora curvula*: conidium; **H.** *Lunulospora cymbiformis*: conidium; **I.** *Margaritispora aquatica*: conidia and conidiophore; **J.** *Mycocentrospora acerina*: conidium; **K.** *Mycofalcella calcarata*: conidium; **L.** *Naiadella fluitans*: conidium; **M.** *Pyramidospora casuarinae*: conidia and conidiophores; **N–O.** *Pyramidospora densa*: conidia and conidiophore. (Scale bar: A,C–O= 20 µm; B= 40 µm)

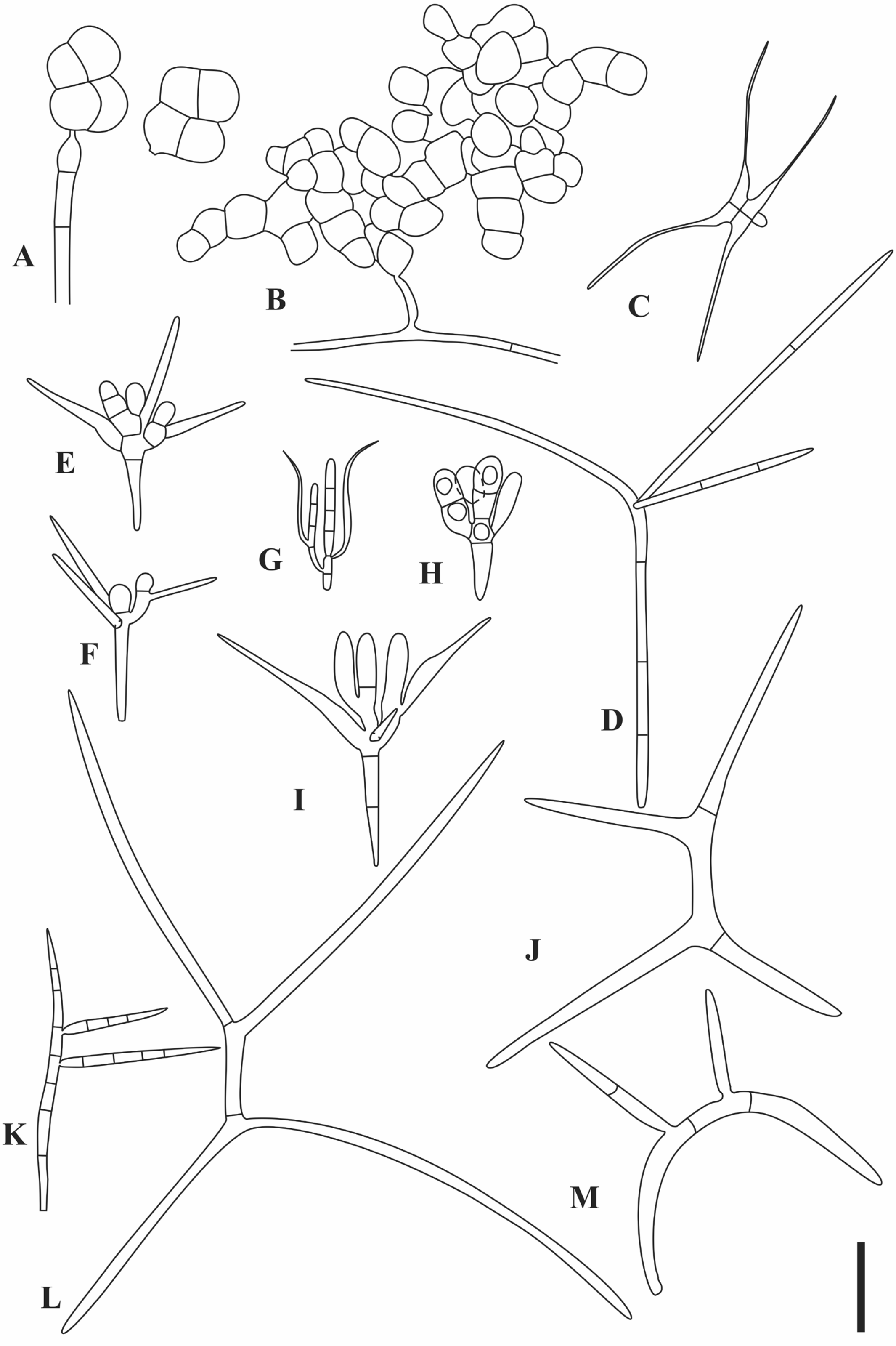

FIGURE 6. A. *Pyramidospora quadricelullaris*: conidia and conidiophore; **B.** *Pyramidospora robusta*: conidium and conidiophore; **C.** *Scutisporus brunneus*: conidium; **D.** *Tetrachaetum elegans*: conidium; **E.** *Tetracladium breve*: conidium; **F.** *Tetracladium marchalianum*: conidium; **G.** *Tetracladium maxiliiforme*: conidium; **H.** *Tetracladium nainitalense*: conidium; **I.** *Tetracladium setigerum*: conidium; **J.** *Tricladium angulatum*: conidium; **K.** *Tricladium attenuatum:* conidium; **L.** *Tricladium chaetocladium*: conidium; **M.** *Tricladium curvisporum*: conidium. (Scale bar: A–E, G–M= 20 µm; F= 40 µm)

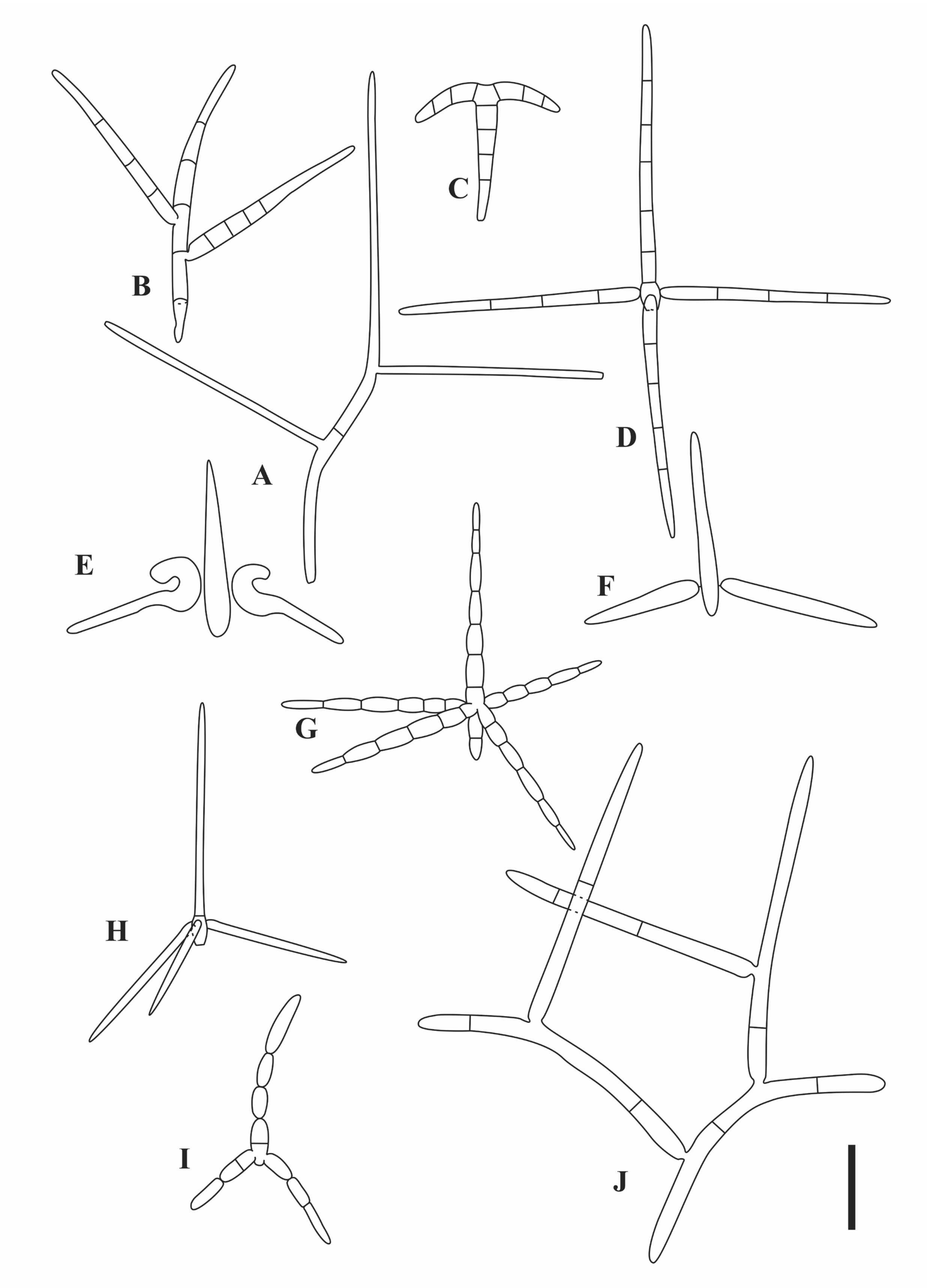

FIGURE 7. A. *Tricladium gracile*: conidium; **B.** *Tricladium splendens*: conidium; **C.** *Trinacrium incurvum*: conidium; **D.** *Triscelophorus acuminatus*: conidium; **E.** *Triscelophorus curviramifer*: conidium; **F.** *Triscelophorus deficiens*: conidium; **G.** *Triscelophorus magnificus*: conidium; **H.** *Triscelophorus monosporus*: conidium; **I.** *Trisulcosporium acerinum*: conidium; **J.** *Varicosporium elodeae*: conidium. (Scale bar: A–B, D, G–J= 20 µm; C= 25 µm; E–F= 10 µm)

Notes:—*Pyramidospora* was erected with *P. casuarinae* as a type species, and it currently comprises nine species (Oliveira *et al.* 2015). *Pyramidospora casuarinae* is easily distinguished from other species of the genus by conidia having a pyramidal shape, 3–4 cells produced as outgrowths from the original basal cell and from the top cell (Nilsson 1962a). In Brazil, three species of *Pyramidospora* were recorded: *P. casuarinae* from the Atlantic Forest on submerged leaves (Schoenlein-Crusius *et al.* 2009), *P. robusta* C.G. Moreira & Schoenl.-Crus. (2012: 523) from the Atlantic Forest on submerged leaves of *Caesalpinia echinata* Lam. (1785: 461) and *Campomanesia phaea* (O. Berg.) Landrum (1984: 241) (Moreira & Schoenlein-Crusius 2012) and *P. quadricellularis* M.S. Oliveira, Malosso & R.F. Castañeda-Ruiz (2015: 973) on submerged leaves from the Atlantic Forest (Oliveira *et al.* 2015). *Pyramidospora casuarinae* is a new record to the Caatinga.

Triscelophorus monosporus Ingold, Trans. Br. Mycol. Soc. 26:152, 1943.
(Fig. 7H)

Material examined:—BRAZIL. Bahia: Piatã, Chapada Diamantina, on submerged leaves of *Calophyllum brasiliense* (*Calophyllaceae*)*,* 10 July 2014, *P.O. Fiuza s.n* (HUEFS 215907).

Conidia tetraradiate, hyaline, comprised by the main axis and three branches attached to its basal cell, main axis 1-septate, tapering toward the apex, not constricted at the septum, apical cell 45–60 × 3.5–4 µm; doliiform basal cell with truncated base, 5–7 × 4.5–5 µm; branches cylindrical, slightly constricted at the base, aseptate, 37–45 × 2.5–3 µm.

Geographical distribution:—Cosmopolitan.

Notes:—*Triscelophorus monosporus* is the type of the genus composed by eight species (Matsushima 1993). The conidia of *T. monosporus* are similar to *T. acuminatus* Nawawi (1975: 346), both have a slightly tapering main axis with doliiform basal cell, but in the latter, the axis is multiseptate, while in *T. monosporus* it is typically 1-septate (rarely with no septum). In Brazil, five species of *Triscelophorus* (Table 2) have been recorded, including *T. monosporus* from the state of São Paulo. *Triscelophorus monosporus* is a new record to the Caatinga.

Key to species of Ingoldian fungi from Brazil

1. Conidia not branched 2
- Conidia branched 19
2. Conidia filiform, long-fusoid, scolecoid or lunate 3
- Conidia flattened, obovoid or tetrahedral 17
3. Conidia aseptate 4
- Conidia septate 6
4. Conidia lunate with submedian scar, 100–130 × 2.5–5 µm .... *Lunulospora curvula* (Fig. 5G)
- Conidia without submedian scar 5
5. Conidia gently curved, falcate or sigmoid .... *Flagellospora curvula* (Fig. 4H)
- Conidia straight .... *Flagellospora stricta* (Fig. 4I)
6. Conidia with excentric basal extension 7
- Conidia without excentric basal extension 9
7. Conidia less than 5 µm in width .... *Anguillospora filiformis* (Fig. 2C)
- Conidia more than 5 µm in width 8
8. Conidia often with the median cell somewhat larger, scar distinct, truncated, 87–188 × 6–13 µm .... *Mycofalcella calcarata* (Fig. 5K)
- Conidia sometimes fuscous, 150–200 × 6–15 µm .... *Mycocentrospora acerina* (Fig. 5J)
9. Conidia with 0–2 septa 10
- Conidia with more than 2 septa 11
10. Conidia with submedian scar and often inflated in the lower third .... *Lunulospora cymbiformis* (Fig. 5H)
- Conidia without submedian scar, 0–2-septate .... *Aquanectria penicillioides* (Fig. 2F)
11. Conidia bent abruptly at >90° angle 12
- Conidia gently curved 14
12. Conidia kinked 1–2 times 13
- Conidia kinked 3 or more times .... *Condylospora flexuosa* (Fig. 3H)
13. Conidia, 12–15-septate .... *Condylospora spumigena* (Fig. 3J)
- Conidia larger, 22–27 septate .... *Condylospora gigantea* (Fig. 3I)
14. Conidia more than 10 µm wide .... *Anguillospora crassa* (Fig. 2B)
- Conidia less than 10 µm wide 15
15. Conidia with base truncated or with subulate extension 4–23 septate, 50–590 × 3–9.5 µm (schizolytic secession) 16
- Conidia mostly with basal frill or remnants of separating cell (rhexolytic secession), 7–20 septate, 105–345 × 3–5 µm .... *Anguillospora longissima* (Fig. 2E)

16. Conidia 10–23 septate, 60–590 × 4.5–9.5 µm.......... *Anguillospora furtiva* (Fig. 2D)
- Conidia 4–6 septate, 53–90 × 3–5 µm.......... *Filosporella versimorpha* (Fig. 4C)
17. Conidia obovoid, 1-septate, 10–13 × 6.5–8 µm .... *Dactylella microaquatica* (Fig. 3N)
- Conidia not obovoid 18
18. Conidia tetrahedral to subspherical, 10–13 diam .... *Margaritispora aquatica* (Fig. 5I)
- Conidia flattened, triangular, three-lobed, with a pedicellate base .... *Dendrosporium lobatum* (Fig. 3P)
19. Conidia multiradiate, tetraradiate, T or Y shaped.......... 20
- Conidia of other, more complex, shapes 46
20. Conidia multiradiate 21
- Conidia tetraradiate, T or Y shaped 22
21. Conidia with more than 9 branches .... *Flabellospora multiradiata* (Fig. 4F)
- Conidia with less than 9 branches .... *Flabellospora verticillata* (Fig. 4G)
22. Conidia tetraradiate 23
- Conidia T or Y shaped 51
23. Very large conidia with globose to pyramidal central body and four branches .... *Brachiosphaera tropicalis* (Fig. 3B)
- Conidia of another shape 24
24. Conidia with clamps .... *Ingoldiella hamata* (Fig. 5B)
- Conidia without clamps 25
25. Main axis with base dolliform, obpyriform or obclavate 26
- Main axis of another shape.......... 30
26. Main axis with basal cell doliiform or obclavate and 3–5 branches 27
- Main axis with basal cell obpyriform or obclavate and two branches 29
27. Main axis with 3–5 branches, elements constricted at each septum .... *Triscelophorus magnificus* (Fig. 7G)
- Conidial elements are not constricted at each septum.......... 28
28. Conidia multiseptate, with three branches.......... *Triscelophorus acuminatus* (Fig. 7D)
- Conidia 0–1 septate, with three branches .... *Triscelophorus monosporus* (Fig. 7H)
29. Conidia with strongly curved branches .... *Triscelophorus curviramifer* (Fig. 7E)
- Conidia with branches not curved .... *Triscelophorus deficiens* (Fig. 7F)
30. Conidia with a central body and four branches 31
- Main axis cylindrical, clavate, fusiform, straight or curved.......... 32
31. Spherical central body 5–6.3 µm diam., no constrictions at branch insertions .... *Lemonniera alabamensis* (Fig. 5D)
- Spherical central body 4–5 µm diam., branches strongly constricted at the point of insertion .... *Lemonniera pseudofloscula* (Fig. 5F)
32. Elongated main axis with typically two branches arising at different levels 33
- Conidia of different shape 38
33. Main axis and lateral branches are markedly attenuated, main axis 46.5–69 × 2.3 µm.......... *Tricladium attenuatum* (Fig. 6K)
- Main axis and lateral branches are not markedly attenuated.......... 34
34. Main axis is bent at lateral branch insertions, branches are not constricted at the base.......... 35
- Main axis is not bent at lateral branch insertions, branches constricted at the base.......... 36
35. Branches tape distinctly toward the apex .... *Tricladium angulatum* (Fig. 6J)
- Branches thinner than main axis, of uniform width .... *Tricladium gracile* (Fig. 7A)
36. Main axis fusiform, 60–120 × 6–7 µm, 3–6 septate, 30–80 × 6–7 µm .... *Tricladium splendens* (Fig. 7B)
- Main axis not fusiform 37
37. Main axis with 2–3 branches, strongly curved, 28–45 × 1.5–3 µm .... *Tricladium curvisporum* (Fig. 6M)
- Main axis with 2 branches, curved, 150–200 × 3–4 µm .... *Tricladium chaetocladium* (Fig. 6L)
38. Conidia with two divergent branches attached at the same level near the middle of the main axis 39
- Conidia with 3–5 branches 41
39. Main axis slightly swollen and bent at branch insertion, resulting in conidia appearing as if having a main axis and 3 apical branches .... *Geniculospora inflata* (Fig. 4 J–K)
- Main axis not swollen at branch insertion 40
40. Branches 23–53 × 1.5–2.5 µm.......... *Alatospora acuminata* (Fig. 2A)
- Branches 120–150 × 2–4 µm.......... *Tetrachaetum elegans* (Fig. 6D)
41. Cylindrical axis.......... 42
- Obconic or clavate axis 44
42. Conidia with three branches not constricted at the insertions, attached at the base of the main axis .... *Lemonniera aquatica* (Fig. 5E)
- Conidia with three branches constricted or slightly constricted at the insertions 43
43. Main axis 23–37.5 × 1.5–3 µm, branches 33–90 × 1.5–3 µm.......... *Articulospora tetracladia* (Fig. 3A)
- Main axis 30–60 × 3.5 µm, branches 90–110 × 5–7 µm .... *Flabellocladia tetracladia* (Fig. 4D)
44. Conidia with 3–5 branches, main axis sometimes inconspicuous.......... *Flabellospora crassa* (Fig. 4E)
- Conidia of other shape.......... 45
45. Main axis clavate, 1-septate, branches 50–70 µm long.......... *Clavariopsis aquatica* (Fig. 3G)
- Clavate to obconic axis, aseptate, elements ca. 10 µm long .... *Heliscella stellata* (Fig. 5A)
46. Conidia with cylindrical main axis and >3 lateral branches or with asymmetrical main axis consisting of inflated cells.......... 47
- Conidia papilioniform, or with acicular branches, or with oblong or digitiform elements.......... 58
47. Conidia with cylindrical main axis.......... 48
- Conidia with asymmetrical main axis 53

48. Conidia with multiple branches developing on one side of the axis .... *Varicosporium elodeae* (Fig. 7J)
- Conidia with multiple branches not developing just on one side of the axis 49
49. Lateral branches arise in pars or in whorls of three from near the base of the straight main axis ...... *Dendrospora erecta* (Fig. 3O)
- Lateral branches do not arise in pars or in whorls of three from near the base of the main axis, main axis curved to hook-shaped 50
50. Conidia with a main axis having more than 7 primary lateral branches .... *Dendrosporomyces prolifer* (Fig. 4A)
- Conidia with a main axis having less than 7 primary lateral branches .... *Dendrosporomyces splendens* (Fig. 4B)
51. Conidia T-shaped, main axis slightly club-shaped, branches curved, 18.5–20 µm long .... *Trinacrium incurvum* (Fig. 7C)
- Conidia of different shape 52
52. Conidia with two branches attached close to the base of the axis, septate and strongly constricted at the septa .... *Trisulcosporium acerinum* (Fig. 7I)
- Conidia Y-shaped, with a single short subapical branch 4–8.5 µm long .... *Aquanectria submersa* (Fig. 2G)
53. Asymmetrical main axis with two lateral branches produced by subapical cell 54
- Conidia with strongly curved main axis of deltoid and allantoid cells; overall appearance of four diverging branches 55
54. Main axis 100–200 µm long .... *Culicidospora aquatica* (Fig. 3L)
- Main axis 35–50 µm long .... *Culicidospora gravida* (Fig. 3M)
55. Branches less than 13 µm long .... *Campylospora parvula* (Fig. 3F)
- Branches more than 13 µm long 56
56. Branches 0.5–0.7 µm wide .... *Campylospora filicladia* (Fig. 3E)
- Branches more than 1 µm wide 57
57. Branches more than 30µm long .... *Campylospora chaetocladia* (Fig. 3D)
- Branches less than 30 µm long .... *Campylospora brasiliensis* (Fig. 3C)
58. Conidia with navicular main axis 59
- Conidia papilioniform, with digitiform elements, or with oblong cells 60
59. Conidia with schizolytic secession .... *Jaculispora submersa* (Fig. 5C)
- Conidia with rhexolytic secession .... *Naiadella fluitans* (Fig. 5L)
60. Conidia papilioniform, with four cells and branches attached to each cell of the main body .... *Scutisporus brunneus* (Fig. 6C)
- Conidia with digitiform elements or oblong cells 61
61. Cells of conidia tightly arranged to form a pyramid-like compact structure 62
- Main axis with digitiform, ellipsoid and acicular elements 65
62. Main axis composed of two cells with 8–13 lateral branches .... *Pyramidospora robusta* (Fig. 6B)
- Conidia with 2–8 branches 63
63. Conidia with 6–8 branches, spanning 29–37 µm .... *Pyramidospora densa* (Fig. 5 N-O)
- Conidia composed of globose or oblong cells 64
64. Conidia composed of four globose cells .... *Pyramidospora quadricellularis* (Fig. 6A)
- Conidia composed of 3–5 rounded cells .... *Pyramidospora casuarinae* (Fig. 5M)
65. Main obconic axis with two digitiform and an ellipsoid element .... *Tetracladium nainitalense* (Fig. 6H)
- Main axis with 2–3 acicular branches 66
66. Main axis with two acicular branches .... *Tetracladium maxilliformis* (Fig. 6G)
- Main axis with three acicular branches 67
67. Main axis with two ellipsoid elements 3–6 µm wide .... *Tetracladium marchalianum* (Fig. 6F)
- Main axis with 3 digitiform elements 68
68. Digitiform elements 10–13.5 × 3.5 µm and acicular branches 12–35 × 2–3.5 µm .... *Tetracladium breve* (Fig. 6E)
- Digitiform elements 12–15 × 3–9 µm and acicular branches 20–40 × 3 µm .... *Tetracladium setigerum* (Fig. 6I)

Discussion

Ingoldian fungi comprise about 320 species distributed worldwide. In Brazil, 85 taxa have been recorded from four out of six Brazilian biomes: Atlantic Forest (53 taxa), Caatinga (39 taxa), Cerrado (21 taxa) and Amazon (19 taxa) (Fig. 1). The Atlantic Forest currently shows the highest diversity, which could be explained by both the number and the length of studies. Indeed, it had the highest number of studies (18, with 15 of them in the state of São Paulo), and they originated more than 27 years ago. On the other hand, the Caatinga had only five studies distributed in four states during just five years; the Cerrado biome was addressed in two studies (all in São Paulo state) since 1999; and the Ingoldian fungi from the Amazon were sampled in two studies (two states) only starting from 2014 (Figs. 8–9). Pampa and Pantanal biomes have not yet been sampled for the Ingoldian fungi (Fig. 8). Bärlocher & Boddy (2015) argue that freshwater wetlands may be the hotspots of fungal diversity. Taking into account that the Pantanal biome is one of the largest continuous wetland habitats on the planet (MMA 2016), mycological expeditions to this area are critically needed.

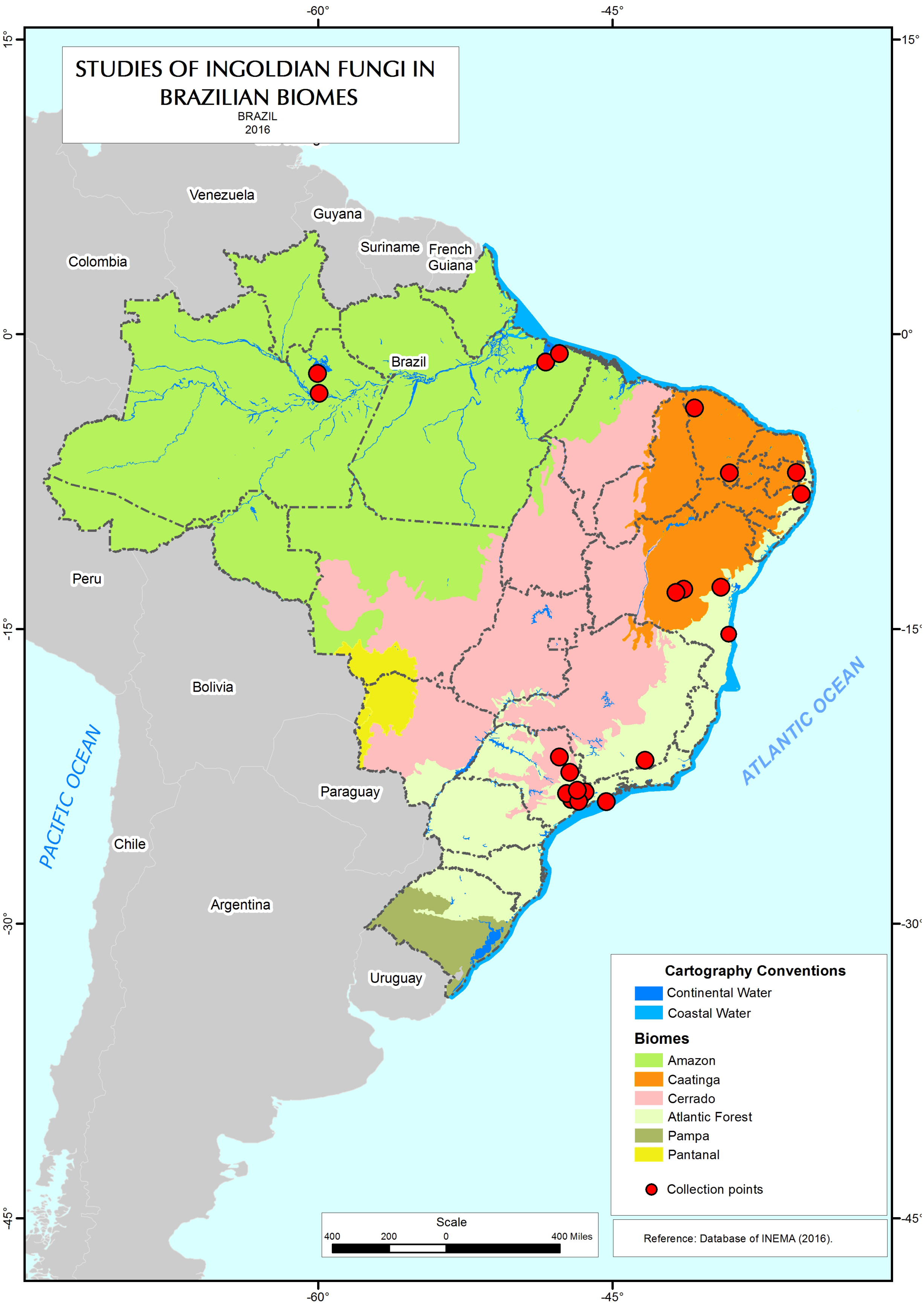

FIGURE 8. Distribution of collection sites of Ingoldian fungi in Brazil.

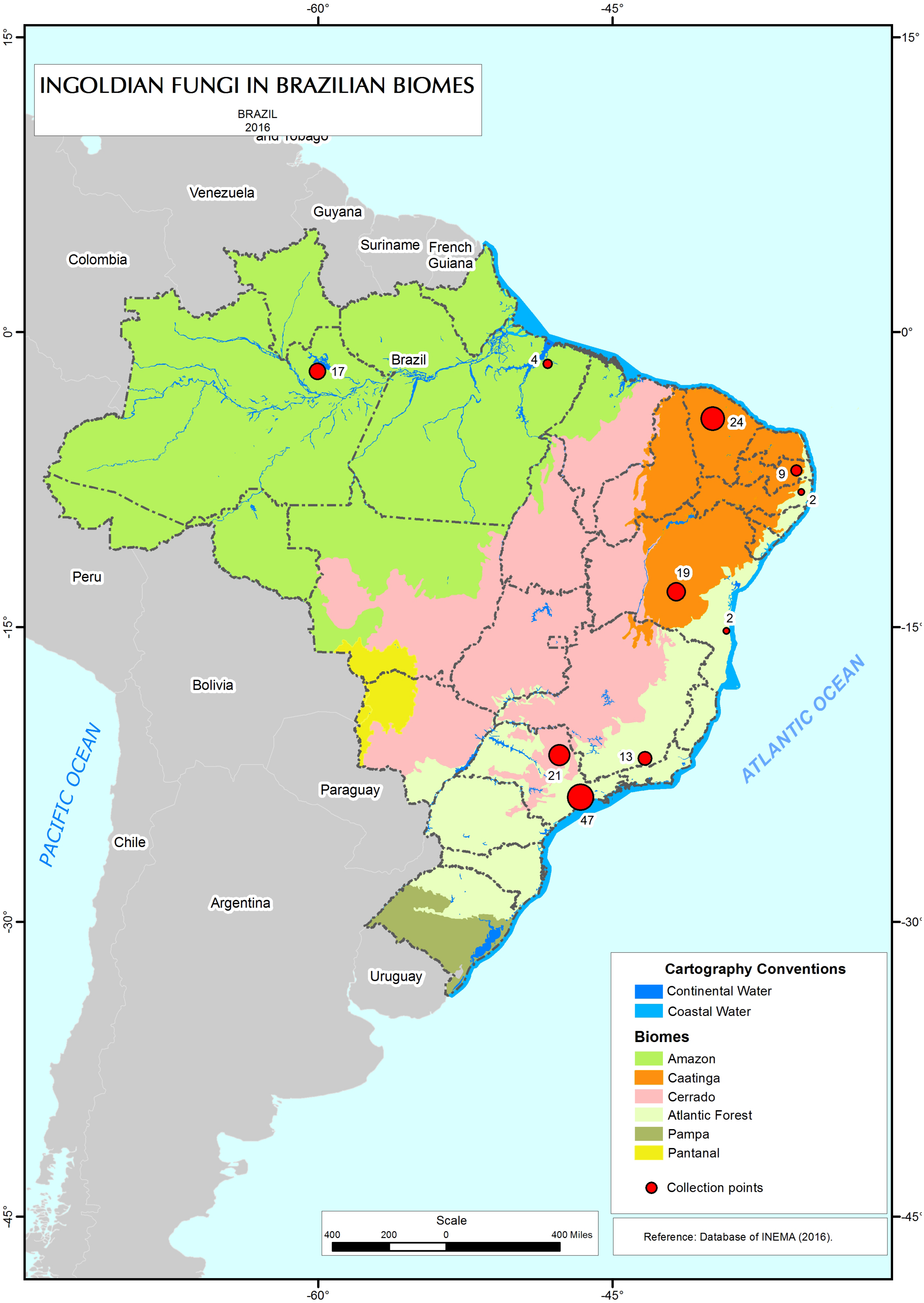

FIGURE 9. Taxa richness of Ingoldian fungi at different sites in Brazilian biomes. The size of the symbol corresponds to the number of taxa recorded from a particular site.

In the Atlantic Forest and the Cerrado, the Ingoldian fungi have been recorded from incubated submerged leaves or randomly collected leaf litter (Schoenlein-Crusius & Grandi 2003, Schoenlein-Crusius *et al.* 2009), while during the studies in the Caatinga and the Amazon, these fungi have been recorded from foam samples or incubated submerged leaves, leaf petioles and bark (Fiuza & Gusmão 2013a, Fiuza *et al.* 2015). The differences in the techniques employed may have contributed to the ability to detect certain species of the Ingoldian fungi. For example, litter bag approach often employing leaf litter of a single type may negatively affect our ability to detect species with pronounced substrate specificities compared to studies relying on randomly collected naturally occurring mixtures of leaves from multiple tree species. While examining foam can quickly provide a reasonable snapshot of community structure based on spores of Ingoldian fungi in transport, this approach complicates fungal isolation into pure culture that may be sometimes necessary for reliable identification.

Among 85 taxa of Ingoldian fungi recorded from Brazil, 27 are unique to the Atlantic Forest, 18 to the Caatinga, 5 to the Amazon and 3 to the Cerrado (Fig. 1). This can be explained by the unequal number of studies on Ingoldian fungi in these biomes as well as by biogeography (Figs. 8–9). However, some common species, such as *Anguillospora longissima* (Sacc. & P. Syd.) Ingold (1942: 402) and *Flagellospora curvula* are reported from all Brazilian biomes with relatively high frequency (Table 2). These are cosmopolitan species that were previously often reported from other countries in both temperate and tropical climates (Shearer 1992, Sridhar *et al.* 2010, Sudheep & Sridhar 2011).

The present study that focused on the submerged leaves of *C. brasiliense* yielded three new records to Brazil and two new records to the Caatinga. *Dendrosporomyces prolifer* has been confirmed to have tropical to subtropical distribution, while *Flagellospora stricta* and *Geniculospora inflata* have been recorded just in the temperate regions until now.

Studies of the Ingoldian fungi in the Atlantic Forest have been conducted primarily in the urban areas (Schoenlein-Crusius *et al.* 2015b), where some water bodies experience eutrophication (Schoenlein-Crusius & Milanez 1989, Schoenlein-Crusius *et al.* 2009). Nevertheless, some species reported from these impacted sites are also found in relatively pristine streams e.g. *Anguillospora longissima, A. filiformis* Greath. (1961: 202) and *Flagellospora curvula* (Fiuza & Gusmão 2013a, Fiuza *et al.* 2015). On the other hand, *Naiadella fluitans* Marvanová & Bandoni (1987: 579) has been recorded just from Brazilian urban areas (Shoenlein-Crusius *et al.* 2015b).

Brazil has many species of Ingoldian fungi that are also reported from other tropical countries such as Malaysia (Nawawi 1985b) and Puerto Rico (Santos-Flores & Betancout-López 1997), and tropical to subtropical areas of India (Sridhar *et al.* 1992, Sudheep & Sridhar 2013). These countries share genera like *Condylospora* Nawawi (1976: 363), *Flabellospora* Alas. (1968a: 415), *Flabellocladia* Nawawi (1985c: 174), *Ingoldiella* D.E. Shaw (1972: 258) and *Jaculispora* H.J. Huds. & Ingold (1960: 475), which are not common in temperate zones.

The studies of the Ingoldian fungi in Brazil in the last 13 years (after Schoenlein-Crusius & Grandi 2003) added 54 taxa to the list, which now contains 85 taxa. This demonstrates a drastic shift in our understanding of the diversity of the Ingoldian fungi in Brazil. However, there are still huge gaps in our data from many regions and totally unexplored biomes (Fig. 8), requiring further studies on the biodiversity of the Ingoldian fungi and their potential application in biotechnology.

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