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THE DIVERSITY OF AQUATIC HYPHOMYCETES IN SOUTH AMERICA

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MINI REVIEW

ABSTRACT

Aquatic Hyphomycetes, also named Ingoldian or freshwater fungi, constitute a group of anamorphic fungi that are typically aquatic, producing tetraradiate, sigmoid or spherical conidia on submerged plant debris (leaf litter, petioles, bark, etc.). Mainly occurring in lotic systems, these fungi are considered to be one of the most active groups of organisms in the decomposition of leaf litter, and play a crucial role in the trophic chain. In South America, aquatic Hyphomycetes are mentioned for Argentina, Brazil, Chile, Ecuador, Peru and Venezuela, totalizing the report of about 90 species. Almost all studies are taxonomical, some with proper drawings and complete descriptions, but no keys have been provided yet, nor there is a specific culture collection for preserved strains. The published papers are still sporadic and dispersed, emphasizing a great need to improve the knowledge of the diversity of South American aquatic Hyphomycetes. The present review contents the check list of reported species until now, and has the aim to encourage the research concerned with aquatic Hyphomycetes in non explored regions of the continent.

Key-words: anamorphic fungi, aquatic Hyphomycetes, biodiversity, Brazil, South America.

INTRODUCTION

The group of the aquatic Hyphomycetes comprises fungi that produce conidia exclusively in the aquatic environment or in the interstitial water among soil particles. Their habitats are preferencially streams with clear, clean, well-aerated waters, with moderate turbulence, and also reservoirs and lakes with different kinds or levels of pollution. The conidia may be trapped in foam, dispersed in the water, floating on the water surface or are associated to organic decomposing substrates as leaf litter and twigs (36).

From the taxonomical point of view, the aquatic Hyphomycetes constitute an artificial phylogenetically heterogenous group, being anamorphs of Ascomycota and Basidiomycota (1,60). Identification of the species has been mainly based on the morphological features of the conidia (40,60).

The term “tetraradiate fungi” has been also frequently used to name this fungal group because many species produce conidia with a radiate or star-like shape, build by a central part, from which three or four arms are projected in divergent positions (18,59). The hydrodynamic shapes of the conidia confers to these fungi higher ability to remain suspended in the water for extended periods of time and improve the chances of the propagules to become attached to organic substrates, available for colonization. However, among the aquatic Hyphomycetes there are species that produces sigmoid, fusiform, coiled and spherical conidia too, which are also dependent of the aquatic environment to complete their life cycle (22,40).

This fungal group has been also named “Ingoldian fungi” in honour to Prof. Dr. C. T. Ingold, who was one of the most important pioneers in the study of aquatic Hyphomycetes (18). The eminent Professor studied these fungi in several aquatic environments in the United Kingdom and other countries starting from 40’s, describing species that are now considered cosmopolitan (36,40).

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According to their form and life-cycle, a classification of the freshwater fungi (22) into the following groups was proposed: Ingoldian Hyphomycetes (fungi that present conidia with hydrodynamic shape and are exclusively dependent on aquatic environment for reproduction); aero-aquatic Hyphomycetes (fungi that may support submerged conditions but reproduce out of aquatic environments), and terrestrial-aquatic Hyphomycetes and submerged-aquatic Hyphomycetes, which are observed in aquatic and terrestrial environments as facultative organisms. One year later three groups were better distinguished among the former: Ingoldian fungi, aero-aquatic fungi and lignicolous aquatic fungi (21). In the present revision representants of all these group were considered.

In tropical and equatorial climates the leaf litter and the soil are constantly wetted by heavy daily rainfalls, which may reach more than 3,000 mm/year in certain regions. In such conditions, it can be difficult to distinguish aquatic from terrestrial fungi only on basis of the habitat.

It has been observed that some typical geofungi isolated from such areas, like *Epicoccum nigrum* Link and *Trichoderma viride* Rifai are able to produce spores in submerged cultures (51). *Beltrania, Camposporium, Chaetendophragmia, Cladosporium, Cryptophiale, Dactylella, Dictyochaeta, Kionochaeta, Phaeoisaria, Subulispora, Tetraploa* and other well-known terrestrial genera of Hyphomycetes are usually found on submerged litter as "facultative aquatic fungi" (21). On the other hand, some typical aquatic species such as *Sporidesmium* and *Articulispora* has been isolated from non aquatic environments. One can speculate about the reason for this behavior, considering the possibility of adaptations or tolerance of the fungi to drastic habitat changes and/or climatic conditions of the ecosystem.

Fact is that, besides of the polemic discussion about which fungi are truly aquatic and if the terrestrial fungi may keep their saprophytic hability even in submerged conditions, the recognition of the importance of the aquatic Hyphomycetes has been continuously increased since many years. These fungi are considered predominant in the leaf decomposition process in aquatic environments. There is an evidence that aquatic Hyphomycetes are able to degrade several plant cell polymers such as cellulose, hemicellulose, pectin (16) and probably lignin (35,40), producing amylase, cellulase, pectinase, protease, pyrocatechol oxidase, triacyl glycerol lipase and xylanase (17,40,58).

Such degradative enzymes may cause breakdown of leaf tissues and increase the palatability to leaf-eating invertebrates, besides their biomass is an important component in the diet of aquatic invertebrates (9,18,57,58). Some aquatic fungi are able to degrade animal parts like insect exoskeletons, hair and fish scales (22).

Excellent considerations and descriptions of methods to perform ecological studies concerning aquatic Hyphomycetes may be consulted in Bärlocher (9), Suberkropp (58), Dix and Webster (18) and Marvanová (40).

During the autumn in temperate climates, streams receive a great supply of tree leaves which may be densily colonize by a high diversity of aquatic Hyphomycetes (9). In the tropics the richness of these fungi is probably influenced by the type of substrates, chemical and physical changes in the streams (35) as well as due complex interactions among several climatic and limnological factors (9,40). Thus, it has been considered that in the tropics, the analysis of the seasonal behavior of these fungi may be more difficult (50).

Based on accumulative results of several worldwide studies, about 100 anamorphic genera and 300 species of aquatic Hyphomycetes are known until now (37).

In the revision for tropical freshwater Hyphomycetes Goh (21) listed 19 taxa to South America without specifying the countries. The quantification of the taxa in revisions concerned with fungal diversity in the tropics may result different numbers in function of several definitions of aquatic fungi and also depends on the availability of the literature. There may be many interesting additional data in regional journals, monographs, thesis and reports.

As the aquatic Hyphomycetes has been characterized as one of the most active fungi in the mineralization of leaf litter, and consequently important dynamizers of the nutrient cycling in the aquatic environments, it has been considered relevant to increase the knowledge of the species diversity in terms of geographic distribution.

The aim of this revision is to present the state of the art of the studies concerned with aquatic Hyphomycetes in Brazil, in the context of South America, to encourage the conduction of surveys in unexplored areas of the continent.

SOUTH AMERICA

For South America, reports of aquatic Hyphomycetes are low and mainly from Argentina, Chile, Ecuador, Peru, Venezuela (Table 1) and Brazil (Table 2).

In Argentina the sampling of submerged mixed leaf litter, leaves of definied species such as *Salix* sp., *Nothofagus dombeyi*, *N. pumillio*, foam, wood, cork and plant debris, mainly from sites at Santiago River and Tierra Del Fuego, resulted in the report of about 25 fungal taxa (Table 1).

Dead leaves of *Nothofagus dombeyi* (Mirb.) Blume sampled at Negro River, Nahuel Huapi National Park were analysed and the aero-aquatic fungus *Candelabrum spinulosum* v. Bev. was described (19). *Campylospora chaetocladia* Ranzoni, *Clathrosphaerina zalewskii* v. Bev. and *Gyoerffyella gemellipara* Marvanová were described from leaves of *Nothofagus pumilio* (Poepp. et Endl.) Oerst. and foam samples taken from streams in Neuquén, San Martín de los Andes (2). Among the mycota associated with grass leaves, dicotyledoan

leaf litter, wood and foam samples, 12 aquatic Hyphomycetes were reported in some streams and lakes in Tierra del Fuego (20).

Surveys were performed in the subtropical region of Santiago River in Buenos Aires (5,6,7), resulting in the description of 19 Hyphomycetes including nine new species and one new combination, *Dictyochaeta assamica* (Agnihothrudu) Arambarri, Cabello and Mengascini. Furthering the studies with Hyphomycetes from Santiago River, Cabello *et al*. (13) described *Camposporium antillanum* Castañeda Ruiz and Cazau *et al*. (15) published two new species: *Dwayaangam gamundiae* Cazau, Arambarri and Cabello and *Diplocladiella taurina* Cazau, Arambarri and Cabello. The taxonomical descriptions are complete and well documented by drawings. Besides, several other studies were performed at several localities in Argentina, involving the sampling of leaf litter or woody debris, from which many not typical aquatic fungi were isolated (3,4,11,12,14).

In Chile (Table 1), samples of wood, leaf litter and insects were collected in several streams and lakes in the temperate region of Osorno (10). The authors observed 14 taxa of Ingoldian fungi, identified nine at specific level and documented their taxonomic features by spore drawings.

Table 1. Aquatic Fungi (Hyphomycetes) reported from South America.

a) Argentina

Species	Substrates	Localities	Authors
Actinospora megalospora Ingold	Grass leaves and foam samples	Tierra del Fuego (Olivia River and Pipo River)	20
Anavirga laxa Sutton	Leaf litter	Tierra del Fuego (Tohluin)	20
Anguillospora longíssima (Sacc. et Sydow) Ingold	Grass leaves, leaf litter, dicotiledonean leaves and foam	Tierra del Fuego (Pipo River, Cabecera Fagnano, Yehuin and Puerto Harberton)	20
Articulospora tetracladia Ingold	Foam samples	Tierra del Fuego (Pipo River, Olivia River and Campamento Don Bosco)	20
Beverwykella pulmonaria *(van Beverwijk) Tubaki*	Plant debris in freshwater	Buenos Aires (Santiago River)	5
Camposporium antillanum Castañeda Ruiz	Submerged leaf litter	Buenos Aires (Santiago River)	13
Campylospora chaetocladia Ranzoni	Submerged leaves of *Nothofagus pumilio* (Poepp. Et Endl.) Oerst., *Acer* sp. and foam samples	San Martin de los Andes (Neuquén)	2
Candelabrum spinulosum v. Beverwijk	Submerged leaf litter of *Nothofagus dombeyi* (Mirb.) Blume	Negro River	19
Casaresia sphagnorum (Fragoso) Perrott	Leaf litter and wood	Tierra del Fuego (Pipo River, Olivia River, Turhera Garibaldi)	20
Clathrosphaerina zalewskii v. Beverwijk.	Submerged leaf litter of *N. pumilio*	San Martin de los Andes (Neuquén)	2
Clavariana aquatica Nawawi	Leaf litter	Tierra del Fuego (Cabecera Fagnano)	20
Clavariopsis aquática de Wild.	Leaf litter and foam	Tierra del Fuego (Tohluim and Campamento Don Bosco)	20
Clavatospora longibrachiata	Foam samples	Tierra Del Fuego (Pipo River and Turhera Garibaldi)	20
Dictyochaeta assamica (Agnihothrudu) Arambarri, Cabello and Mengascini	Decaying leaf litter	Buenos Aires (Santiago River)	5
Dictyochaeta gamundii Arambarri *et* Cabello	Rotten cork samples	Buenos Aires (Santiago River)	6
Diplocladiella taurina Cazau, Arambarri *et* Cabello	Submerged leaf litter	Buenos Aires (Santiago River)	15
Dwayaangam gamundiae Cazau, Arambarri *et* Cabello	Submerged leaf litter	Buenos Aires (Santiago River)	15
Gyoerffyella gemellipara	Submerged leaves of *N. pumilio*, *Salix* sp., *Liriodendron tulipifera*, *Camelia japonica* L. and foam	San Martín de los Andes (Neuquén)	2
Isthmolongispora asymmetrica Arambarri *et* Cabello	Decaying leaf litter on water surface	Buenos Aires (Santiago River)	6
Lemonniera aquática de Wild.	Foam samples and dicotiledonean leaves	Tierra del Fuego (Cabecera Fagnano, Pipo River and Campamento Don Bosco)	20
Lunulospora curvula Ingold	Dicotiledonean leaves	Tierra del Fuego (Puerto Harberton)	20
Mycocentrospora acerina (Hartig) Deighton	Foam samples	Tierra del Fuego (Puerto Harberton)	20
Subulispora Argentina Arambarri et Mengascini	Decaying leaf litter	Buenos Aires (Santiago River)	7
Tetracladium setigerum (Grove) Ingold	Dicotiledonean leaves	Tierra del Fuego (Puerto Harberton)	20
Tetraploa abortiva Arambarri *et* Cabello	Decaying leaf litter	Buenos Aires (Santiago River)	7
Tetraploa aristata Berkeley et Broome	Plant debris and submerged branches covered by petroleum	Buenos Aires (Santiago River)	5

b) Chile

Species	Substrates	Localities
Actinospora sp.	Wood, leaf litter and insects	Osorno Province (Laguna El Encanto)
Alatospora acuminata Ingold	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River, Chanleufu River, Puleufu River, Toro Lake, Laguna El Encanto)
Anguillospora sp.	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River, Chanleufu, Puleufu)
Articulospora sp.	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River, Puleufu, Toro Lake)
Clavariopsis aquática de Wildeman	Wood, leaf litter and insects	Osorno Province (Chanleufu River)
Heliscus lugdunensis Sacc. *et* Therry	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River)
Lunulospora curvula Ingold	Wood, leaf litter and insects	Osorno Province (Puleufu River)
Margaritispora aquática Ingold	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River)
Tetrachaetum elegans Ingold	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River, Puleufu, Toro Lake)
Tetracladium marchalianum de Wildeman	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River)
Tetracladium setigerum (Grove) Ingold	Wood, leaf litter and insects	Osorno Province (Laguna El Encanto)
Tricladium sp.	Wood, leaf litter and insects	Osorno Province (Pilmaiquén River)
Tricladium splendens Ingold	Decaying organic matter	Osorno Province (Damas River)
Triscelophorus sp.	Wood, leaf litter and insects	Osorno Province (Puleufu River)

Observation: all reports are from Burgos & Riffart (10)

c) Ecuador

Species	Substrates	Localities
Campylospora filicladia Nawawi	Decaying plamae petioles, leaf litter, submerged fruit	Yuturi River
Dwayaangam cornuta Descals	Decaying broad leaves	Cuyabeno
Isthmolongispora intermedia Matsushima	Decaying palmae petioles and wood of broad-leaved-tree	Cuyabeno
Scutisporus brunneus Ando and Tubaki	Decaying leaves of tangarana ponga	Yuturi River
Tripospermum porosporiferum Matsushima	Broad leaved leaf litter	Cuyabeno

Observation: all reports are from Matsushima (41)

d) Peru

Species	Substrates	Localities
Camposporium antennatum Harkn.	Decaying palmae petioles	Tambopata
Campylospora filicladia Nawawi	Decaying palmae petioles, leaf litter, submerged fruit	Tambopata, Yalapa River, Monanti River
Condylospora spumigena Nawawi	Decaying twigs of broad-leaves	Ampiyacú River
Dactylella aphrobrocha Drechsler	Decaying palmae petioles	Tambopata Reserv
Dactylella brochopaga Drechsler	Decaying palmae petioles	Manu Reserv
Dactylella cionopaga Drechsler	Decaying palmae petioles	Momon River
Dactylella doedycoides Drechsler	Decaying palmae petioles	Tambopata Reserv
Dactylella ellipsospora W. B. Grove	Decaying palmae petioles	Tambopata Reserv
Dactylella eudermata Drechsler	Decaying palmae petioles	Negro River
Dactylella heterospora Drechsler	Decaying palmae petioles	Momon River
Dactylella musiformis (Drechsler) Mat.	Decaying palmae petioles	Tambopata Reserv, Manu and Monanti River
Diplocladiella scalaroides Arnaud	Decaying *Inga* sp. fruit	Monanti River
Dwayaangam cornuta	Decaying broad leaves	Cuyabeno
Isthmolongispora intermédia Mat.	Decaying palmae petioles and wood of broad-leaved-tree	Yalapa River
Isthmolongispora mínima Mat.	Decaying palmae petioles	Negro River
Isthmolongispora quadricellularia Mat.	Decaying palmae petioles	Tambopata Reserv
Isthmolongispora rotundata Mat.	Decaying palmae petioles	Tambopata Reserv
Isthmotricladia laeensis	Decaying leaves of Oje	Yalapa River
Naiadella fluitans	Decaying palmae petioles	Tambopata Reserv
Speiropsis pedatospora Tubaki	Decaying leaves of rifare	Itaya River
Tetraploa aristata Berk. and Br.	Decaying palmae leaflets	Sinchicuy River
Tetraploa ellisii Cooke	Leaf lesions of *Oryza sativa*	Aucayaco River
Tricladium sp.	Forest soil	Yarapa River
Trinacrinum angamosense Mat.	Decaying palmae petioles	Colônia Angamos
Tripospermum myrti (Lind.) Hughes	Decaying palmae petioles	Aucayaco River
Tripospermum porosporiferum Mat.	Broad leaved leaf litter	Momon River
Triscelophorus curviramifer Mat.	Broad leaved leaf litter	Negro River
Triscelophorus deficiens Mat.	Decaying palmae leaves	Sinchicuy River
Varicosporium elodeae Kegel	Decaying leaves of Oje	Monanti River

Observation: all reports are from Matsushima (41)

e) Venezuela

Species	Substrates	Localities
Anguillospora longissima (Sacc. and Sydow) Ingold	Submerged leaf litter	Streams in the Andes
Angulospora aquatica S. Nilsson	Submerged decaying leaves	Estado Bolívar (Pool under a waterfall in Cerro Venamo)
Articulospora tetracladia Ingold	Submerged leaf litter	Caracas (streams in the surroundings)
Campylospora chaetocladia Ranzoni	Branches of *Casuarina* and on decaying leaves	Caracas (streams in the surroundings)
Dactylella aquatica Ingold	Submerged leaves	Caracas (mountain region around the city)
Flagellospora penicillioides Ingold	Submerged leaf litter	Streams in the Andes
Heliscus submersus H. J. Hudson	Submerged leaf litter	Caracas (Los Chorros River)
Lunulospora curvula Ingold	Submerged leaf litter	Streams in the northern coastal mountains
Pyramidospora casuarinae S. Nilsson	Tiny branches of a *Casuarina* species and petioles of leaves	Caracas (Los Chorros River)
Tetracladium marchalianum de Wildeman	Submerged leaf litter	Caracas (small stream near the water reservoir at Mariposa)
Triscelophorus monosporus Ingold	Submerged leaf litter	Streams in the Andes

Observation: - all reports are from Nilsson (44)

Table 2. Check-list of aquatic Hyphomycetes reported in Brazil.

	Substrates	Localities	Ref.
Alatospora acuminata Ingold	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
Alatospora sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
Anguillospora crassa Ingold	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
	Mixed leaf litter	Stream in a forest (Rio Claro, SP)	48
	Mixed leaf litter	Stream (Águas de Lindóia, SP)	48
	Leaves of *Alchornea triplinervia* Spreng. M. Arg.	Stream in Paranapiacaba (Santo André, SP)	48
	Mixed leaf litter	Stream (Itirapina, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	47
A. longissima (Sacc. et Syd.) Ingold	Leaves of *Ficus microcarpa* L. f.	Lake in the Botanical Garden (São Paulo, SP)	53
	Laves of *Quercus robur* L.	Lake (Itapecerica da Serra, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
	Mixed leaf litter	Stream (Jataí, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Mixed leaf litter	Stream (Itirapina, SP)	46
	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	47
Anguillospora sp.	Leaves of *A.triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *F. microcarpa*	Lake in the Botanical Garden (São Paulo, SP)	53
	Leaves of *Q. robur*	Lake (Itapecerica da Serra, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
Articulospora tetracladia Ingold	Leaves of *Q. Robur*	Lake (Itapecerica da Serra, SP)	53
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	48
	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
Camposporium antennatum Harkn.	Leaves of *C. fissilis*	Soil surface at the Uiversity of São Paulo (São Paulo, SP)	30
	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
Camposporium pellucidum (Grove) Hughes	Mixed leaf litter	Stream (Jataí, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Leaves of *Q. Robur*	Artificial lake (Itapecerica da Serra, SP)	52
	Leaves of A. *triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
Campylospora chaetocladia Ranzoni	Mixed leaf litter	Waterfall (Águas de Lindóia, SP) and Stream (Rio Claro, SP)	48
	Mixed leaf litter	Stream (Itirapina, SP)	46
Campylospora parvula Kuzuha	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Campylospora sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
Centrospora acerina (Hartig) Newhall	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	38
Clavariopsis aquatica De Wild.	Mixed leaf litter	Waterfall (Águas de Lindóia, SP)	48
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Clavariopsis sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38

Cont.

Clavatospora stellata (Ingold and Cox) Nilsson ex Marvanová and Nilsson	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Dactyella submersa (Ingold) Nilsson	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
Dactylella sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
Dendrospora sp.	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
Dendrosporomyces splendens (Nawawi) Nawawi	Leaves of *A. triplinervia*	Soil surface at Paranapiacaba (Santo André, SP)	27
	Leaves of *Euterpe edulis* Mart.	Soil surface at Paranapiacaba (Santo André, SP)	28
Dictyochaeta fertilis Hughes and Kendrick	Roots of *Calathea stromata* Sond	Soil surface at the Botanical Garden (São Paulo, SP)	23
	Roots of *Maranta bicolor* Ker	Soil surface at the Botanical Garden (São Paulo, SP)	24
	Roots of *Ctenanthe oppenheimiana* Sond.	Soil surface at the Botanical Garden (São Paulo, SP)	25
	Roots of *Stromanthe sanguinea* Sond.	Soil surface at the Botanical Garden (São Paulo, SP)	26
Flabellopsora crassa Alasoadura	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
	Mixed leaf litter	Stream (Itirapina, SP)	46
Flagellospora curvula Ingold	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	38
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Flagellospora penicillioides Ingold	Mixed leaf litter	Stream (Luís Antônio, SP)	46
Flagellospora sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
Helicosporium sp.	Water and soil	Streams ("igarapés") in a forest at the Federal University of Manaus (Manaus, AM)	56
Heliscella stellata (Ingold et Cox) Marv. et Nilsson	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
Heliscus submersus H. J. Hudson	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Heliscus sp.	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
Ingoldiella hamata Shaw	Mixed leaf litter	Stream (Itirapina, SP)	46
Isthmotricladia sp.	Leaves of *Q. Robur*	Artificial lake (Itapecerica da Serra, SP)	52
Lemmoniera aquatica De Wild.	Leaves of *Q. robur*	Artificial lake (Itapecerica da Serra, SP)	52
	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *Q. robur*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Leaves of *F. microcarpa*	Lake in the Botanical Garden (São Paulo, SP)	47
	Leaves of *T. pulchra*	Stream in Paranapiacaba (Santo André, SP)	43
Lemonniera sp. *(terrestris?)*	Mixed leaf litter	Soil of the cerrado forest (Corumbata, SP)	8
Lunulospora curvula *Ingold*	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Monjolinho River (São Carlos, SP)	38
	Leaves of *Q. robur*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Monjolinho River (São Carlos, SP)	39
	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
	Mixed leaf litter	Stream in a *Pinus* spp forest (Rio Claro, SP)	48
	Mixed leaf litter	Stream (Águas de Lindóia, SP)	48
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	48
	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
	Mixed leaf litter	Stream in a "cerrado" reserve (Jataí, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Mixed leaf litter	Stream (Itirapina, SP)	46
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	51
	Leaves of *Q. robur*	Lake (Itapecerica da Serra, SP)	52
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Leaves of *T. pulchra*	Stream in Paranapiacaba (Santo André, SP)	43
Lunulospora cymbiformis *Miura*	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
	Mixed leaf litter	Stream (Jataí, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
Lunulospora sp.	Leaves of *F. microcarpa*	Lake in the Botanical Garden (São Paulo, SP)	47
	Leaf litter	Monjolinho River (São Carlos, SP)	38
Kionochaeta ramifera (Matsushima) P. M. Kirk and B. Sutton	Leaves of *Cedrela fissilis*	Soil surface in a forest at the University of São Paulo (São Paulo, SP)	30
	Leaves of *A. triplinervia*	Soil surface in the atlantic rainforest of "Juréia-Itatins" (Peruíbe, SP)	29
	Leaves of *A. triplinervia*	Soil surface at Paranapiacaba (Santo André, SP)	27
	Leaves of *E. edulis*	Soil surface at Paranapiacaba (Santo André, SP)	28

Cont.

Margaritispora sp.	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *Q. robur*	Stream in Paranapiacaba (Santo André, SP)	53
Margaritispora aquática Ingold	Leaves of *T. pulchra*	Stream in Paranapiacaba (Santo André, SP)	43
Monotosporella microaquatica (Tubaki) S. Nilsson	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Monotosporella sp.	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	38
Phaeoisaria clematidis (Fckl.) Hughes	Leaves of *A. triplinervia*	Soil surface at "Juréia-Itatins" (Peruíbe, SP)	29
	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
Speiropsis irregularis Petersen	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Speiropsis scopiformis Kuthubutheen and Nawawi	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
	Leaves of *T. pulchra*	Soil surface at Paranapiacaba (Santo André, SP)	31
Sporidesmiella hyalosperma (Corda) P. M. Kirk var Hyalosperma P. M. Kirk	Roots of *C. Stromata*	Botanical Garden (São Paulo, SP)	23
	Roots of *C. oppenheimiana*	Botanical Garden (São Paulo, SP)	25
	Roots of *S. sanguinea*	Botanical Garden (São Paulo, SP)	26
	Leaves of *E. edulis*	Soil surface at Paranapiacaba (Santo André, SP)	28
	Leaves of *T. Pulchra*	Soil surface at Paranapiacaba (Santo André, SP)	31
Subulispora longirostrata Nawawi and Kuthubutheen	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
	Leaves of *T. pulchra*	Soil surface at Paranapiacaba (Santo André, SP)	31
	Several types of leaf litter	Several localities in the State of São Paulo	32
Subulispora procurvata Tubaki	Several types of leaf litter	Several localities in the State of São Paulo.	32
	Leaves of *A. triplinervia*	Soil surface at "Juréia-Itatins" (Peruíbe, SP)	29
	Leaves of *A. triplinervia*	Soil surface at Paranapiacaba (Santo André, SP)	27
	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
	Leaves of *T. pulchra*	Soil surface at Paranapiacaba (Santo André, SP)	31
Tetrachaetum elegans Ingold	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *Q. robur*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	48
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	51
	Leaves of *Q. robur*	Lake (Itapecerica da Serra, SP)	52
	Leaves of *F. microcarpa*	Lake in the Botanical Garden (São Paulo, SP)	47
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Stream (Itirapina, SP)	46
Tetraploa aristata Berkeley and Broome	Roots of *C. oppenheimiana*	Botanical Garden (São Paulo, SP)	25
	Roots of *Stromanthe sanguinea*	Botanical Garden (São Paulo, SP)	26
Trichodochium sp	Leaves of *Q. robur*	Lake (Itapecerica da Serra, SP)	52
Tricladium gracile Ingold	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
Tricladium sp.	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	38
Tripospermum camelopardus Ingold, Dann et Mac Dougall	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
Tripospermum myrti (Lind.) S. J. Hughes	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
	Mixed leaf litter	Stream (Itirapina, SP)	46
	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
	Leaves of *T. pulchra*	Stream in Paranapiacaba (Santo André, SP)	43
Tripospermum sp.	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	51
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *Q. Robur*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	38
Triscelophorus magnificus Petersen	Leaves of *Q. robur*	Lake in Itapecerica da Serra, SP	52
Triscelophorus monosporus Ingold	Leaves of *F. microcarpa*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *Q. robur*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Waterfall (Rio Claro, SP)	48
	Mixed leaf litter	Stream in a forest (Rio Claro, SP)	48
	Mixed leaf litter	Waterfall (Águas de Lindóia, SP)	48
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	48
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	51
	Leaves of *Q. robur*	Lake (Itapecerica da Serra, SP)	52
	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Mixed leaf litter	Dam "Represa do Guarapiranga" (São Paulo, SP)	39
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39

Cont.

	Mixed leaf litter	Stream (Mogi-Guaçú, SP)	46
	Mixed leaf litter	Stream (Jataí, SP)	46
	Mixed leaf litter	Stream (Luís Antônio, SP)	46
	Mixed leaf litter	Stream (Itirapina, SP)	46
	Leaves of *T. pulchra*	Stream in Paranapiacaba (Santo André, SP)	43
	Mixed leaf litter	Dam "Represa do Guarapiranga" in São Paulo, SP	39
Triscelophorus sp.	Mixed leaf litter	Monjolinho River in São Carlos, SP	38
	Mixed leaf litter	Monjolinho River and Jacaré River (São Carlos, SP)	39
Trisulcosporium acerinum Hudson et Sutton	Leaves of *A. triplinervia*	Stream in Paranapiacaba (Santo André, SP)	53
	Leaves of *C. fissilis*	Soil surface at a rainforest in Maringá (Paraná)	33
Wiesneriomyces laurinus (Tassi) P. M. Kirk	Leaves of *M. cabussu*	Soil surface at Paranapiacaba (Santo André, SP)	34
	Leaves of *T. pulchra*	Soil surface at Paranapiacaba (Santo André, SP)	31

Matsushima (41,42) greatly contributed to the knowledge of Hyphomycetes in South America. Several decaying palmae petioles mainly but also leaf litter, fruits and soil samples were collected in the vicinity of some rivers in the equatorial Amazon region of Ecuador and Peru. In Ecuador (Table 1) 5 species were reported (41). Many fungi with star-like conidia or considered aquatic were isolated but it is not clear if they were obtained from really submerged substrates.

In Peru 30 taxa were described (42). Among them, 8 known species considered aquatic to Ingold (36) or Marvanová (40) were found, including *Campylospora filicladia* Nawawi and *Condylospora spumigena* Nawawi and also new taxa such as *Isthmolongispora biramifera* Matsushima, *Triscelophorus curviramifer* Matsushima, *Trinacrium incurvum* Matsushima, *Trinacrium angamosense* Matsushima, *Trinacrium* sp. (MPF-9P323), and one new combination, *Triscelophorus deficiens* (Matsushima) Matsushima. The Hyphomycetes were fully described and documented through excellent photographs and drawings.

In Venezuela (Table 1) 11 taxa of aquatic Hyphomycetes were isolated from submerged leaf litter, branches and petioles of *Casuarina* in streams, pools and waterfalls in the surroundings of Caracas (44). 2 new genera and 2 new species were proposed: *Angulospora aquatica* S. Nilss. and *Pyramidospora casuarinae* S. Nilss., with complete descriptions and drawings.

BRAZIL

In Brazil studies of aquatic Hyphomycetes in freshwater were initiated at the end of the 80's mainly in the state of São Paulo (Table 2). Thus, some species were observed during fungal decomposition of leaves of *Ficus microcarpa* L. f. submerged in an artificial lake in the "Parque Estadual das Fontes do Ipiranga", municipality of São Paulo (47). Later, aquatic Hyphomycetes were observed during the decomposition of leaves of *Quercus robur* L. in a lake in the municipality of Itapecerica da Serra (52). In the "cerrado" (a kind of Brazilian savannah), municipality of Corumbataí, a strain of *Lemonniera* was found in terrestrial leaf litter (8).

The first reports, besides the observation of fungi in mixed leaf litter collected in waterfalls ("Cachoeira do Altarújo", municipality of Rio Claro) and streams ("Recanto dos Nefelibatas", municipality of Águas de Lindóia) are mentioned in the taxonomical description of the Brazilian species (48,49). Besides some interesting aquatic Hyphomycetes, such as *Dictyochaeta fertilis* Hughes and Kendrick, *Sporidesmiella hyalosperma* (Corda) P. M. Kirk var. *hialosperma* P. M. Kirk and *Tetraploa aristata* Berkeley and Broome were isolated from Marantaceae roots in the "Parque Estadual das Fontes do Ipiranga" (23,24,25,26).

Camposporium antennatum Harkn. and *Kionochaeta ramifera* (Matsushima) P. M. Kirk and B. Sutton were observed during the decomposition of leaves of *Cedrela fissilis* Vell. in the urban Forest reservation of the University of São Paulo (30). On the same plant species, but in the reservation of "Horto Florestal Dr. Luiz Teixeira Mendes", in the municipality of Maringá, State of Paraná, *Wiesneriomyces laurinus* (Tassi) P. M. Kirk was reported (33).

At the surface of the leaves of *Alchornea triplinervia* (Spreng.) M. Arg., in the forest reservation of "Juréia-Itatins" *Kionochaeta ramifera*, *Phaeoisaria clematidis* (Fckl.) Hughes and *Subulispora procurvata* Tubaki were observed (29).

In the "Reserva Biológica do Alto da Serra de Paranapiacaba", municipality of Santo André, many species of aquatic Hyphomycetes were observed during the fungal succession on decomposing submerged leaves of *A. triplinervia* (51). In the same region, the mycota associated with leaves of *Ficus microcarpa*, *Alchornea triplinervia* and *Quercus robur* were compared, evaluating the diversity (53), the methods for fungal quantification to express the colonization intensity (45) and the correlation between fungal diversity (zoosporic fungi and aquatic Hyphomycetes) and macro and microelements during the decomposition (54,55).

In the same Reserve, *Dendrosporomyces splendens* (Nawawi) Nawawi, a typical species from water, was isolated from *Alchornea triplinervia* and *Euterpe edulis* Mart. leaf litter (27,28). More recently 9 taxa were isolated from decomposing

leaves of *Miconia cabussu* (34). On *Tibouchina pulchra* leaves six Hyphomycetes were observed on leaves (31) and 11 were involved in the fungal succession during the decomposition of submerged leaf litter (43).

Studies of aquatic Hyphomycetes and zoosporic fungi associated with submerged leaf litter in the "cerrado" region were intensified through surveys conducted in the Monjolinho River in the municipality of São Carlos in the State of São Paulo (38). Afterwards, the fungal diversity, biomass production and ergosterol content of submerged leaves were compared between the Monjolinho River and Jacaré-Guaçú River (lotic system) and the reservoir Represa do Guarapiranga (lentic system) in the city of São Paulo. The results were not clear in relation to the correlation between ergosterol / biomass content and fungal diversity, but the aquatic Hyphomycetes were more frequent in the rivers than in the reservoir regardless to the eutrophization level of the environments (39).

A survey of aquatic Hyphomycetes in four "cerrado" regions in the State of São Paulo was concluded recently, obtaining 14 taxa, with three new records for Brazil (46).

Recently, a taxonomical revision of some species of *Subulispora* (*S. longirostrata*, *S. procurvata* and *S. rectilineata*) was accomplished base on the reports of collections of leaf litter at several localities of the State of São Paulo (32).

Until now, almost all sites are situated mainly in the state of São Paulo, approaching collections in streams, rivers of medium size, waterfalls, lakes and reservoirs in subtropical climatic conditions. Although the number of taxa and studies are higher in Brazil than in other South American countries, no new species have been described until now. Also the quality of the taxonomical descriptions and drawings must be improved.

The Brazilian Amazonian region, where water bodies are plenty is still almost unknown. Only 1 record, *Helicosporium* sp. has been cited until now (56).

Comparing the results among the countries, one may observe that some species such as *Anguillospora longissima* (Sacc. and Sydow) Ingold, *Articulispora tetracladia* Ingold, *Clavariopsis aquatica* Wildeman, *Lunulospora curvula* Ingold, and *Triscelophorus monosporus* Ingold are commonly mentioned as they are in other subtropical and tropical areas.

Since in many countries no data about this fungal group have been published, and the studies are very scarce, sporadic and dispersed, it is difficult to draw conclusions about the geographic distribution of aquatic Hyphomycetes in South America.

In Brazil, as well as probably in other countries of South America, the interest of researchers and students in the taxonomy of aquatic Hyphomycetes has come from the observation of the species in ecological studies about leaf litter decomposition and fungal succession. However, the scarcity of taxonomical keys with tropical species and the difficulty of obtaining cultures on agar media has disencouraged further initiatives. Marvanová (40) published a key to tropical and subtropical species but it was based on Indian and Malaysian material. So, the publication of keys and the improvement of the isolation techniques of these fungi in tropical waters may stimulate the interest of more taxonomists in the systematics and ecology of aquatic Hyphomycetes.

Considering the dimension of the Continent, with the high variability of vegetation, habitats and abundance of rivers, streams and waterfalls, the number of aquatic Hyphomycetes in South America, around 90, is still very low. More effort is needed in terms of surveys and taxonomical studies to improve the knowledge of these fungi.

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RESUMO

A diversidade dos Hyphomycetes aquáticos nas águas continentais da América do Sul

Os Hyphomycetes aquáticos, também denominados fungos "Ingoldeanos", constituem grupo de fungos anamórficos tipicamente aquáticos, que produzem conídios tetrarradiados, sigmóides ou esféricos sobre substratos vegetais submersos (folhedo, pecíolos, cortiça, etc.). Ocorrendo principalmente em sistemas lóticos, estes fungos são considerados como um dos grupos de organismos mais ativos na decomposição de folhedo, assumindo papel crucial na cadeia trófica. Na América do Sul os Hyphomycetes aquáticos são mencionados para a Argentina, Brasil, Chile, Equador, Peru e Venezuela, totalizando a citação de aproximadamente 90 espécies. Quase todos os estudos são taxonômicos, com ilustrações adequadas e descrições completas, porém ainda não foram elaboradas chaves sistemáticas ou coleções de culturas de linhagens específicas. Os artigos publicados ainda são esporádicos e dispersos, enfatizando-se a grande necessidade de aperfeiçoamento dos conhecimentos sobre a diversidade dos Hyphomycetes aquáticos na América do Sul. A presente revisão contém listas das espécies mencionadas até o momento e tem o objetivo de encorajar a pesquisa destes fungos em áreas ainda não investigadas no continente.

Palavras-chave: fungos anamórficos, Hyphomycetes aquáticos, biodiversidade, Brasil, América do Sul.

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