



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS

**DIVERSIDAD DE CILIADOS (ALVEOLATA: CILIOPHORA) EN BROMELIAS DE LA
REGIÓN NEOTROPICAL. TAXONOMÍA, ECOLOGÍA Y DISTRIBUCIÓN**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

CARLOS ALBERTO DURÁN RAMÍREZ

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P r e s e n t e

Me permito informar a usted que, en la reunión virtual del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **29 de junio de 2020** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **DURÁN RAMÍREZ CARLOS ALBERTO** con número de cuenta **300630866** con la tesis titulada **“Diversidad de ciliados (Alveolata: Ciliophora) en bromelias de la región neotropical. Taxonomía, ecología y distribución”**, realizada bajo la dirección de la **DRA. ROSAURA MAYEN ESTRADA**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

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“POR MI RAZA HABLARÁ EL ESPÍRITU”
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por ser parte de esta historia

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RESUMEN

Las bromelias cuya morfología permite la formación de una fitotelma, constituyen un hábitat donde se establecen comunidades de ciliados. El objetivo de la presente tesis fue registrar la riqueza específica y determinar la influencia de algunas variables ambientales sobre la comunidad de ciliados que habitan en bromelias epífitas y terrestres en diferentes tipos de vegetación de la Región Neotropical de México, durante los años 2014 a 2016, así como realizar una compilación de las especies registradas en las bromelias del resto del Neotrópico. Para cumplir con estos objetivos, se recolectaron muestras de 189 plantas. Como resultados, se presentan datos del registro de 48 especies de ciliados en 27 especies de bromelias presentes en cinco tipos de vegetación y algunos agroecosistemas cafetaleros en los estados de Chiapas, Hidalgo, Jalisco, Oaxaca, Puebla, Veracruz y Yucatán, México. Se obtuvo que en más del 95% de las plantas analizadas se registró al menos una especie de ciliado, siendo ocho especies nuevos registros de ciliados para México. Los resultados obtenidos reflejaron que el mayor número de especies de ciliados se registraron en las bromelias del bosque tropical caducifolio de la Reserva de la Biosfera Chamela Cuixmala, Jalisco, durante la temporada húmeda de los años 2015 y 2016, principalmente en bromelias que no son tipo tanque o que poseen fitotelmata poco desarrollada como *Bromelia karatas* y *Tillandsia makoyana* donde se destacó la presencia de las formas libre nadadoras de ciliados, y el resto fueron formas sésiles pertenecientes a la subclase Peritrichia. Las especies *Drepanomonas revoluta*, *Glaucomides bromelicola*, *Leptopharynx bromeliophilus* y *Tetrahymena* sp. fueron las más frecuentes que se registraron en el estudio. Se determinaron algunos aspectos ecológicos sobre la comunidad de ciliados en distintas especies de bromelias a lo largo de un gradiente de elevación con fragmentos de bosque de pino, mesófilo de montaña, tropical subcaducifolio y agroecosistemas cafetaleros del centro de Veracruz. Se observó que las comunidades de ciliados tuvieron una composición diferente de acuerdo al tipo de vegetación, y junto con la altitud sobre el nivel del mar y la temperatura del agua en las bromelias, constituyeron los tres principales factores que influyeron sobre la misma. Asimismo, se registró la mayor riqueza específica de ciliados en las bromelias del bosque mesófilo de montaña, donde a su vez fueron más frecuentes las especies de ciliados ‘endémicos’ (referidos como especies que sólo son exclusivas de bromelias) como *Glaucomides bromelicola*. Se presenta además un listado taxonómico que compila 170 especies de ciliados que han sido registradas en bromelias de diez países de la Región Neotropical. La mayoría son especies de las clases Oligohymenophorea, Colpodea y Spirotrichea. Los registros correspondieron a 52 especies de bromelias tanto epífitas como terrestres. México y Brasil contaron con el mayor número de especies. *Bromeliothrix metopoides* y *Glaucomides bromelicola* fueron las especies de ciliados con la mayor distribución a escala geográfica en las bromelias neotropicales. De éstas, algunas especies sólo han sido registradas en bromeliáceas de México, o bien, en algunas islas antillanas y otras únicamente se han observado en bromelias sudamericanas. Predominaron las especies libre nadadoras y junto con las formas sésiles, representaron aproximadamente el 2% del total de las especies conocidas para todo el phylum Ciliophora. De ellas, 16 se han catalogado como habitantes exclusivos de bromelias, pero sin mostrar alguna especificidad por determinada especie de bromelia. El resto de las especies de ciliados, en su mayoría son de distribución cosmopolita por ser frecuentes en ambientes como el suelo, musgos, espeletias y cuerpos de agua dulce, con una predominancia de especies bacterívoras.

ABSTRACT

Bromeliads with tank morphology enable the development of a phytotelm, which is considered a suitable habitat for the establishment of ciliate communities. The objective of this thesis was to record the species richness and to evaluate the influence of some environmental variables on the ciliate community that inhabit in epiphytic and terrestrial bromeliads from different types of forests in the Mexican Neotropics during the years 2014-2016, and to carry out a compilation of all the available ciliate species records from bromeliads, and their distribution along the Neotropical Region. To accomplish these objectives, a total of 189 plants were sampled. As a result of the present study, 48 ciliates species were recorded from 27 bromeliad species in five types of vegetation and some coffee lands from the states of Chiapas, Hidalgo, Jalisco, Oaxaca, Puebla, Veracruz and Yucatán, Mexico. More than 95% of the analyzed plants contained at least one ciliate species, and eight ciliate species were recorded for the first time in Mexico. The largest number of ciliates species was recorded in bromeliads from the dry tropical forest in the Reseve of the Biosphere Chamela Cuixmala, Jalisco, during the humid season of 2015 and 2016, specially in tank-less bromeliads or bromeliads with a poorly-developed phytotelm, like *Bromelia karatas* and *Tillandsia makoyana*, where free-living ciliate species were more common in relation to the sessile ones, which belonged to the sublass Peritrichia. The species *Drepanomonas revoluta*, *Glaucomides bromelicola*, *Leptopharynx bromeliophilus* and *Tetrahymena* sp. were the most frequent in the study. Some ecological aspects of the ciliate community were evaluated from different bromeliad species along an elevational gradient with fragments of pine forest, montane cloud forest, semideciduous tropical forest and coffee lands, located in Central Veracruz. Ciliate community composition was different depending of the type of forest, where altitude above sea level and water temperature in the bromeliads were identified as the three most important variables influencing the composition of the ciliate community. Species richness was larger in bromeliads from the montane cloud forest, where the so-called endemic ciliates (that inhabit only in bromeliads) like *Glaucomides bromelicola* were more frequent. A compilation of 170 ciliates species recorded in bromeliads from ten Neotropical countries is provided. Most of them are species that belong to the classes Oligohymenophorea, Colpodea and Spirotrichea. Species records were obtained from 52 species of epiphytic and terrestrial bromeliads. Mexico and Brazil showed the largest number of species records. *Bromeliothrix metopoides* and *Glaucomides bromelicola* were the two ciliate species with the widest geographic distribution inhabiting in Neotropical bromeliads. Some species have been recorded only in Mexican bromeliads, others were exclusive of bromeliads that inhabit in the Antillean islands, and others have only been observed from Southamerican bromeliads. Free-living species were more common in bromeliads, and by including sessiles ones, both represent almost the 2% of the total known species of the phylum Ciliophora. Sixteen species have been cataloged as exclusive inhabitants of bromeliads, but there is no evidence of specificity between ciliates and certain bromeliad species. Most of the ciliates that inhabit in bromeliads have a cosmopolitan distribution, because they are conspicuous in soils, mosses, espeletias, and freshwater environments, and most of them are bacteria feeders.

INTRODUCCIÓN GENERAL

Los ciliados pertenecen al Phylum Ciliophora ubicado dentro del clado Alveolata debido a la presencia de alveolos debajo de la membrana, considerado un carácter sinapomórfico que comparten con otros protistas como los Apicomplexa, Colpodellida, Colponemida, Dinoflagellata y Perkinsidae (Adl *et al.*, 2019). Citológicamente, los ciliados se caracterizan principalmente por la presencia de cilios derivados de cinetosomas con tres tipos de microfibrillas asociadas, un dualismo nuclear y la conjugación como proceso sexual. La ciliatura se dispone como somática y oral, en forma de monocinétidas, dicinétidas y policinétidas (Lynn, 1988, 2008).

Dentro del Phylum Ciliophora, se agrupan dos subphyla, once clases, 55 órdenes y aproximadamente 8,000 especies (Lynn, 2008). Del total de especies de ciliados a nivel mundial, alrededor de 4,500 son de vida libre, pero se ha estimado que un 80% de la diversidad de los ciliados permanece aún sin ser descrita (Foissner *et al.*, 2007). En México, se han registrado 1,026 especies (Mayén-Estrada *et al.*, 2019) lo que equivale casi al 12% de la diversidad del Phylum.

Los ciliados pueden ser solitarios o coloniales y presentan un tamaño entre 10-3,000 μm (Jones, 1974). Habitán como organismos de vida libre, ya sea libre nadadores o sésiles, formando parte del plancton de zonas neríticas y oceánicas y del bentos de ambientes marinos, cuerpos de agua dulce (lagos, ríos, cuerpos temporales y manantiales), lagos hipersalinos, ambientes salobres (lagunas costeras y manglares), plantas de tratamiento de aguas residuales, ambientes terrestres (suelos y musgos), semiterrestres o bien, como organismos simbiontes de invertebrados y vertebrados, con quienes incluso establecen hiperfiosis (Sabagh *et al.*, 2011), y en plantas acuáticas y cavidades de algunas plantas terrestres (Lynn, 2008, 2017) como las bromeliáceas.

Las Bromeliaceae son una familia diversa de angiospermas la cual agrupa cerca de 3,543 especies en 73 géneros cuya distribución es casi exclusiva del Neotrópico (Givnish *et al.*, 2007, 2011; Gouda *et al.*, 2015), desde el sur de los Estados Unidos hasta Argentina y las Antillas (Frank *et al.*, 2004; Givnish *et al.*, 2011; Luther, 2006). Las bromeliáceas con morfología tanque captan el agua de lluvia entre las axilas de las hojas dando lugar a la formación de una fitotelma (Frank & Lounibos, 1987), que se define como un cuerpo de agua que se forma entre las inflorescencias, hojas o troncos de plantas y cuya acumulación es suficiente para que se establezcan comunidades de organismos acuáticos como los protistas ciliados (Maguire, 1971).

La diversidad de ciliados que habitan en bromelias de México es poco conocida. Durán-Ramírez *et al.* (2015) registraron 61 especies pertenecientes a ocho clases en dos especies de bromelias epífitas del género *Tillandsia*. Foissner (2010), Foissner & Stoeck (2011), Foissner *et al.* (2011) y Omar & Foissner (2011, 2012) documentaron y describieron algunas especies en *Tillandsia heterophylla* E. Morren del estado de Veracruz como *Bromeliothrix metopoides*, *Cotterillia bromelicola*, *Leptopharynx costatus costatus* y *L. bromeliophilus*.

Dunthorn *et al.* (2012) realizaron un análisis filogenético con especies de ciliados que habitan en las fitotelmata de bromelias, en donde se refieren secuencias genéticas de especies registradas en México. Foissner (2003a, b) y Foissner *et al.* (2003 y 2007) mencionaron que es probable que estas plantas alberguen a cientos de nuevas especies de ciliados implicando un proceso de evolución independiente vinculado a las limitaciones ecológicas propias de este microhábitat y paralelo al origen y diversificación de la familia Bromeliaceae en el Neotrópico.

En la actualidad, se conoce escasamente la influencia que ejercen los factores bióticos y abióticos sobre la composición de las comunidades de ciliados, así como su distribución dentro de diferentes especies de bromelias en distintos tipos de ecosistemas. Algunos estudios previos llevados a cabo en una población de *Aechmea distichanta* a lo largo del margen del Río Paraná, al sur de Brasil, han destacado la importancia del agua principalmente de origen pluvial para la presencia de ciliados en las bromelias, así como la influencia que representa la cercanía a cuerpos de agua dulce sobre la composición de la comunidad (Buosi *et al.*, 2014, 2015).

Se presentan los datos obtenidos de 48 especies de ciliados a partir de 27 especies de bromelias. El mayor número de especies se registró tanto en bromelias que no poseen morfología tanque como en algunas que poseen una fitotelma poco desarrollada en el bosque tropical caducifolio de la Reserva de la Biósfera Chamela Cuixmala en Jalisco durante la temporada húmeda de los años 2015 y 2016, de las cuales, la mayoría son ciliados cosmopolitas que habitan típicamente en suelos. A lo largo de un gradiente de elevación con fragmentos de distintos tipos de vegetación en el Centro de Veracruz, se identificó que el tipo de vegetación, la temperatura y la altitud sobre el nivel del mar, influyeron en la composición de las comunidades de ciliados. En bromelias del bosque mesófilo de montaña se observó una mayor riqueza específica, así como una mayor frecuencia de ciliados exclusivos de las bromelias. Estos resultados, junto con los registros previos disponibles en 52 especies de bromelias de diez países neotropicales, suman 170 especies que constituyen poco más del 2% de todas las especies conocidas para el phylum Ciliophora.

Capítulo I

Durán-Ramírez, C. A. & Mayén-Estrada, R. 2018.
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Ciliate species from tank-less bromeliads in a dry tropical forest and their geographical distribution in the Neotropics

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Abstract

The study of ciliate diversity in tropical environments remains scarce. In Neotropical forests, bromeliads are a common component of the vascular flora; bromeliads with tank morphology intercept rain water and detritus, resulting in the formation of a phytotelm, where heterotrophic protist communities like ciliates can establish. However, it is not known if ciliates inhabit tank-less bromeliads. For this reason, the goal of the present study was to investigate if ciliates can establish between the leaf axils of five terrestrial and epiphytic tank-less bromeliad species in a dry tropical forest in west Mexico. We collected samples of rain water and detritus from the leaf axils during the humid season of years 2015 and 2016. For ciliate taxonomical identification, we used optical microscopy, in vivo observation, and silver impregnation techniques. To summarize information about geographical distribution of ciliates identified at species level in the Neotropics, we provided their records from previous works, at country level with locality and georeferenciation. We recorded 27 taxa of ciliates, where the class Oligohymenophorea contained the largest richness of taxa. *Drepanomonas revoluta*, *Leptopharynx bromeliophilus*, and *Tetrahymena* sp. were recorded from all the species of bromeliads. *Bromelia karatas* was the species that hosted the largest number of ciliate taxa (22). Our results indicated that *Glaucostomum bromelicola*, *Gonostomum bromelicola*, *Leptopharynx bromelicola* and *L. bromeliophilus*, species which are considered endemic to tank bromeliads, can also inhabit tank-less bromeliads. We provided previous records of 19 ciliate species from eleven countries within the Neotropical region, and *Bromeliothrix metopoides* was the species most frequently recorded in Neotropical countries (9). Therefore, tank-less bromeliads can constitute a temporal habitat for ciliates, and function as cysts reservoirs in environments with a pronounced seasonality like dry tropical forests.

Key words: cysts, endemic species, geographical distribution, phytotelm, species richness

Introduction

Neotropical dry forests are well known for their high biodiversity of plants and animals (Ceballos & García 1995); nevertheless, studies about ciliate diversity in tropical environments are scarce and fragmented at global scale. Some studies of terrestrial ciliates have been carried out in tropical forests of Africa (Dragesco & Dragesco Kernéis 1979, 1986). In the Neotropics, Foissner (1995, 1997, 2016) studied ciliate richness from floodplains and soils in the Amazon forest of Brazil, in Costa Rica, and from tropical terrestrial and semiterrestrial environments of Venezuela.

The family Bromeliaceae is an important component of the vascular flora of tropical forests, with ca. 3,543 species. Its distribution is almost restricted to Neotropics (Givnish *et al.* 2007, Gouda & Gouda 2015). Many species of the bromeliad subfamilies exhibit tank morphology (Givnish *et al.* 2014). Their coalescent leaves allow the accumulation of rain water and detritus, leading to the formation of a phytotelm (Maguire 1971), where heterotrophic protist such as ciliates can establish (Foissner *et al.* 2003, Durán-Ramírez *et al.* 2015). Other types of bromeliads are commonly terrestrial and miniaturized epiphytes, better known as nebulophytes or atmospheric forms, having various adaptations such as special hairs over the leaf to capture the mist from the air.

The Reserve of the Biosphere Chamela-Cuixmala (RBCC), located in West Mexico, is the habitat of 28 bromeliad species, most found with epiphytic or terrestrial growth, some with tank morphology, tank-less and atmospehric forms (Espejo-Serna *et al.* 2004). Some bromeliad species, especially from the genus *Tillandsia*, are adapted to dry tropical forests where water is a limited resource due to a pronounced seasonality (Benzig 2000; Reyes-García *et al.* 2012; Trejo 2010).

Ciliates that inhabit bromeliads have only been recorded from species with tank morphology (Buosi *et al.* 2014, Dunthorn *et al.* 2012, Durán-Ramírez *et al.* 2015, Foissner *et al.* 2003), where water in the tanks is the most important factor for ciliate establishment (Buosi *et al.* 2014). Moreover, almost half of the species that can be found in tank bromeliads also inhabit soils of different regions of the world and show the ability to resist desiccation through the formation of cysts (Durán-Ramírez *et al.* 2015; Foissner 1998). However, it is not known if ciliates can establish in tank-less bromeliads that do not form a phytotelm.

The objective of this work was to investigate the richness of ciliates species that can inhabit in terrestrial and epiphytic tank-less bromeliads from the dry tropical forest of the RBCC. We also provided data of the previous records and habitats of the identified species in other localities of the Neotropics, in order to compilate the information from the literature about their geographical distribution of these species.

Methodology

Area of study. Two samplings were conducted during the humid season of years 2015 and 2016 (September and October respectively) at Estación de Biología Chamela-UNAM, located within the territory of the RBCC ($19^{\circ}37'$ – $19^{\circ}59'N$ $100^{\circ}94'$ – $105^{\circ}06'W$), municipality of La Huerta, along the coastal mountain range of Jalisco, West Mexico (fig. 1). The elevation ranges from 0 to 430 m asl and the humid season lasts four months, with an average annual precipitation of 750 mm (García-Oliva *et al.* 1995). The territory covers an area of ca. 32,000 acres and constitutes a portion of a fringe of dry tropical forests along the Mexican Pacific slope.

Sample collection. We collected 19 samples including water and detritus, or only detritus accumulated from the rosettes of five terrestrial and epiphytic tank-less bromeliad species of genera *Bromelia* L. 1753, and *Tillandsia* L. 1753. Epiphytic plants were located about 2.0 m above ground. All plants of year 2015 contained little volumes of rain water accumulated between their leaf axils. With the exception of one plant, bromeliads of year 2016 did not contain rain water. The samples were collected with new plastic pipettes and placed into sterilized Falcon tubes. For bromeliads that did not have water between their leaves, we only collected the detritus by using a fine spatula to carefully remove them over a tray. Both dry and water samples were maintained at room temperature. None of the plants were removed from their habitat. Taxonomical identity of bromeliads was investigated by photoidentification and according to Espejo-Serna & López-Ferrari (2005) and Espejo-Serna *et al.* (2004).

Ciliate identification. To carry out the taxonomical identification of ciliates, we analyzed each one of the water samples at least 48 hours after they were collected and at intervals of two days through the following two weeks. For dry samples, we rehydrated detritus with sterile distilled water one month after they were collected by using the non-flooded Petri dish technique (Foissner 1987a). Both types of samples were used to establish cultures in Petri dishes using drops of the original sample, table water Evian®, and wheat infusion to stimulate bacterial growth (Foissner *et al.* 2003). We observed cytological characters of taxonomical importance *in vivo* (e.g. cell size and shape, position and shape of the cytostome, position and number of the contractile vacuoles) using bright field and differential interference contrast microscopy with a Nikon Labophot-2 microscope equipped with a Nikon Digital Sight DS-L15667 camera. We performed silver impregnation techniques according to the protocols of Foissner (2014), to reveal cytological characteristics. We followed Berger (1999), Certes (1891), Fernández-Galiano & Calvo (1992), Foissner (1987b, 1993, 2010, 2013, 2016), Foissner *et al.* (2011), Guggiari & Peck (2008), Lee *et al.* (2000), Omar & Foissner (2011, 2012a, b, 2014), Penard (1922), and Small (1967) for species identification. We followed the systematics according to Lynn (2008).

Geographical distribution. The circumscription of the Neotropical region in the American Continent was according to Morrone (2017). For geographical distribution and the habitats of ciliates identified at species level, we consulted previous published records from papers, theses as well as original descriptions of some taxa (Aladro-Lubel *et al.* 1990, 2006; Arévalo-Trear 1967; Bovee 1957; Buosi *et al.* 2014; Cruz-Jiménez 2017; Durán-Ramírez *et al.* 2015; Foissner 1995, 1997, 2000, 2010, 2013, 2016; Foissner *et al.* 2003; Foissner *et al.* 2011; Hardoim &

Heckman 1996; Hernández-Anaya 1981; Küppers & Claps 2012a,b, 2016; Madrazo-Garibay & López-Ochoterena 1982, 1985; Méndez-Sánchez 2017; Mondragón-Camarillo 2011; Omar & Foissner 2011; Pauleto *et al.* 2009; Rico-Ferrat 1990; Rondello-Bonatti *et al.* 2016; Sigala-Regalado 2011; Steffens & Wilbert 2002). Some species in Foissner (2013) and Foissner *et al.* (2003) with unique records where the sampling locality was not indicated, were included with a general georeferenciation at country level. Georeferences were obtained from original papers, or we did the georeferencing by using the program Google Earth Pro-2017, through the use of its search tool of localities and places in the map, and the name of the locality referred in the original work.

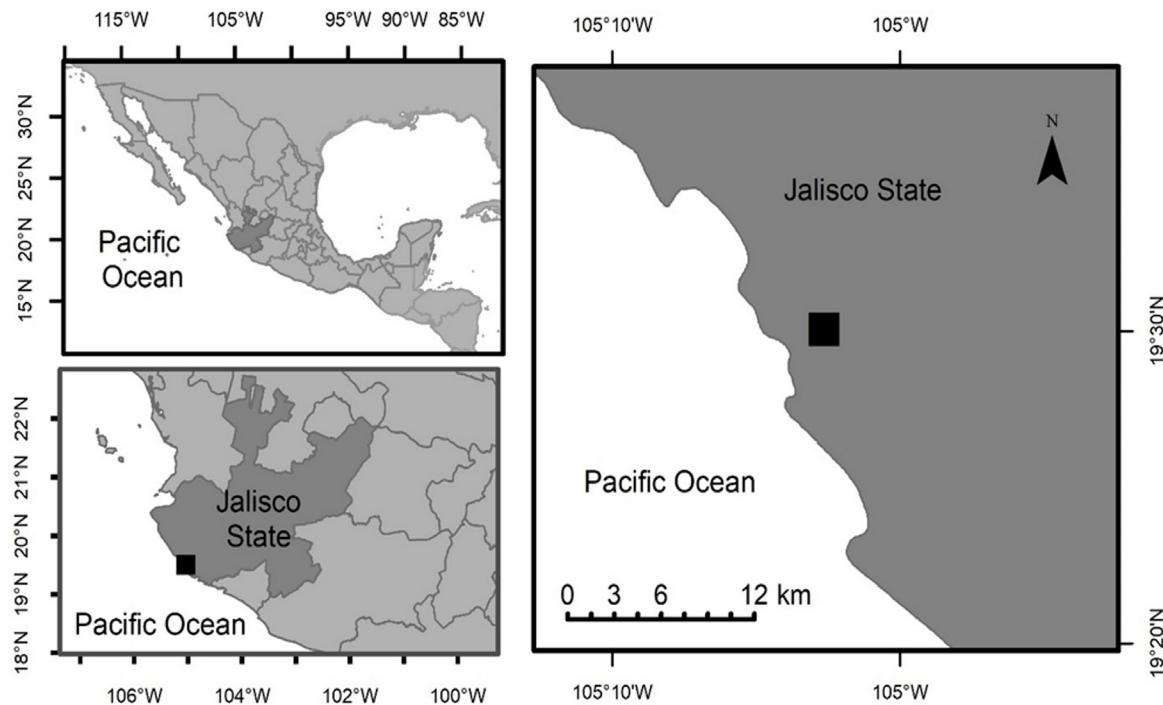


FIGURE 1. Location of the Biosphere Reserve Chamilá-Cuixmala, Jalisco, Mexico.

Results

Ciliate species from tank-less bromeliads. From the bromeliad species *Bromelia karatas* L. 1753, *B. pinguin* L. 1753, *Tillandsia dasyliriifolia* Baker, 1887, *T. polystachia* (L. 1753) L. 1762 and *T. rothii* Rauh, 1976 (fig. 2), we recorded 27 taxa of ciliates, 19 of which were identified at species level. The taxa belonged to six classes as follows: Colpodea (seven taxa), Litostomatea (one taxa), Oligohymenophorea (eight taxa), Phyllopharyngea (one taxa), Nassophorea (six taxa), and Spirotrichea (four taxa) (table 1, fig. 3). From the field samples where little water was found between the leaves, we observed only four species as trophont stages (swimmers and active feeders): *Drepanomonas minuta*, *Epistyis* sp., and *Vorticella* sp. 1 and 2; from samples where detritus were rehydrated, we observed 13 species after their excystment: *Bresslauides terricola*, *Bromeliothrix metopoides*, *Glaucomides bromelicola*, *Gonostomum bromelicola*, *Lambornella* sp., *Leptopharynx brasiliensis*, *L. bromelicola*, *L. bromeliophilus*, *Odontochlamys gouraudi*, *Oxytricha* sp., *Parabryophrya* sp., *Pattersoniella vitiphila* and *Spathidium spatula*, and finally, ten species were recorded as both active or after their excystment (table 1): *Colpoda aspera*, *C. cucullus*, *C. maupasi*, *Cyclidium glaucoma*, *Drepanomonas revoluta*, *Frontonia* sp., *Leptopharynx costatus*, *Paracolpoda steinii*, *Phacodinium metchnikoffi* and *Tetrahymena* sp. We recorded the largest number of ciliate species from *Bromelia karatas* (22). *Drepanomonas revoluta*, *Leptopharynx bromeliophilus* and *Tetrahymena* sp. were recorded from all the bromeliad species.

Bresslauides terricola, *Drepanomonas minuta*, *Leptopharynx brasiliensis*, *Phacodinium metchnikoffi*, and *Spathidium spatula* were recorded inhabiting bromeliads for the first time worldwide. *Bresslauides terricola*, *D. minuta*, *Gonostomum bromelicola*, *L. brasiliensis*, *Pattersoniella vitiphila*, and *P. metchnikoffi* were recorded for the first time in Mexico (Aladro-Lubel *et al.* 2006) (fig. 3). *Bromeliothrix metopoides*, *Glaucomides bromelicola*, *Gonostomum bromelicola*, *Leptopharynx bromelicola*, and *L. bromeliophilus*, species considered as endemic or specific to tank bromeliads, were recorded for the first time in tank-less bromeliads.

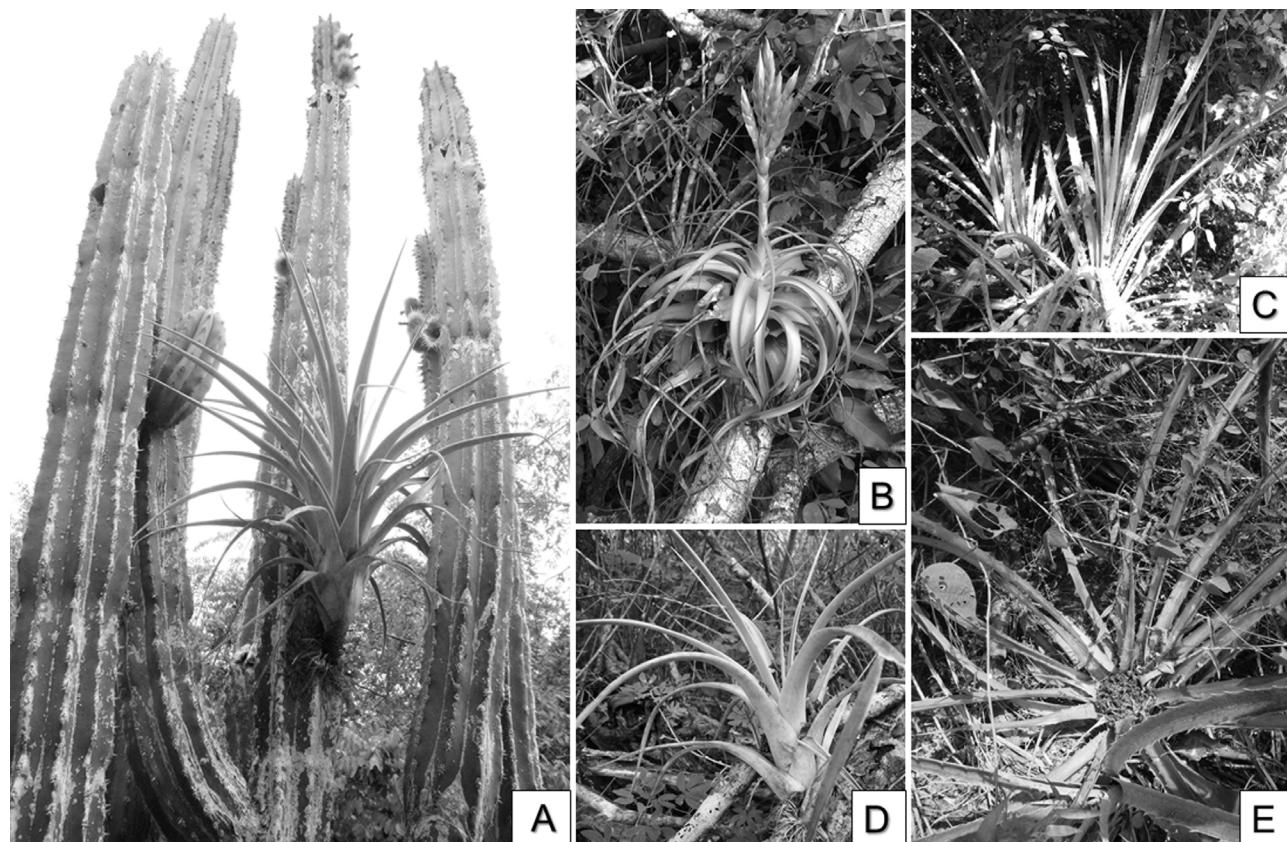


FIGURE 2. Bromeliad species sampled. A=*Tillandsia dasyliriifolia*, B=*T. rothii*, C=*Bromelia pinguin*, D=*T. polystachia* and E=*B. karatas*.

Geographical distribution

Bresslauides terricola (Foissner, 1987b) Foissner, 1993

Foissner, W. 1987b. *Zool. Beitr. N. F.* 31(2):187–282.

Habitat. Biological crusts, soil.

Distribution. **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). **Venezuela:** Amazonas, near town of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Falcón, Morrocoy National Park, near Chichiriviche ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$).

References. Foissner 1995, 2016.

Bromeliothrix metopoides Foissner, 2010

Foissner, W. 2010. *Acta Protozool.* 49(3): 159–193.

Habitat. Moss, tank bromeliads.

TABLE 1. Ciliate species richness from tank-less bromeliads.

Ciliate species	s	Bk	Bp	Td	Tr	Tp	Class ³
<i>Bresslauides terricola</i> ^{1,2}	e	+	-	+	+	-	CO
<i>Bromeliothrix metopoides</i> *	e	+	-	+	-	-	CO
<i>Colpoda aspera</i>	a,e	+	-	+	+	+	CO
<i>Colpoda cucullus</i>	a,e	+	-	+	+	+	CO
<i>Colpoda maupasi</i>	a,e	+	-	+	+	+	CO
<i>Cyclidium glaucoma</i>	a,e	+	-	+	+	+	OL
<i>Drepanomonas minuta</i> ^{1,2}	a	+	-	+	-	+	NA
<i>Drepanomonas revoluta</i>	a,e	+	+	+	+	+	NA
<i>Epistyliis</i> sp.	a	+	-	+	-	-	OL
<i>Frontonia</i> sp.	a,e	+	-	+	+	-	OL
<i>Glaucomides bromelicola</i> *	e	-	-	-	+	-	OL
<i>Gonostomum bromelicola</i> * ¹	e	+	-	+	+	-	SP
<i>Lambornella</i> sp.	e	+	-	-	+	-	OL
<i>Leptopharynx brasiliensis</i> * ^{1,2}	e	+	-	-	+	+	NA
<i>Leptopharynx bromelicola</i> *	e	-	-	-	+	-	NA
<i>Leptopharynx bromeliophilus</i> *	e	+	+	+	+	+	NA
<i>Leptopharynx costatus</i>	a,e	+	-	+	+	-	NA
<i>Odontochlamys gouraudi</i>	e	+	-	+	-	-	PH
<i>Oxytricha</i> sp.	e	-	-	-	+	-	SP
<i>Parabryophrya</i> sp.	e	+	-	-	+	-	CO
<i>Paracolpoda steinii</i>	a,e	+	-	+	+	+	CO
<i>Pattersoniella vitiphila</i> ¹	e	+	-	+	+	-	SP
<i>Phacodinium metchnikoffi</i> ^{1,2}	a,e	+	+	-	+	+	SP
<i>Spathidium spatula</i> ²	e	+	-	+	+	-	LI
<i>Tetrahymena</i> sp.	a,e	+	+	+	+	+	OL
<i>Vorticella</i> sp.1	a	-	-	+	-	-	OL
<i>Vorticella</i> sp.2	a	-	-	+	-	+	OL
Total of ciliate species		22	4	20	21	12	

Bromeliad species: Bk=*Bromelia karatas*, Bp=*Bromelia pinguin*, Td=*Tillandsia dasyliriifolia*, Tr=*Tillandsia rothii*, Tp=*Tillandsia polystachia*.

Ciliate classes: CO=Colpodea, LI=Litostomatea, NA=Nassophorea, OL=Oligohymenophorea, PH=Phyllopharyngea, SP=Spirotrichea.

s=trophic state of ciliate species at the moment of the sampling: a=active, e=encysted.

¹=New record from Mexico.

²=New records of ciliates inhabiting in bromeliads.

³=Clasification system according to Lynn, 2008.

*Species with geographical distribution restricted to the Neotropics.

Distribution. **Brazil:** Paraíba, Nature Reserve Mata do Buraquinho, near the town of João Pessoa ($7^{\circ}08'13.74''S$ $34^{\circ}51'31.35''W$). Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$). **Costa Rica:** ($9^{\circ}54'N$ $84^{\circ}05'W$). **Chile:** ($33^{\circ}27'S$ $70^{\circ}40'W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Ecuador:** ($0^{\circ}00'S$ $78^{\circ}26'W$). **Jamaica:** ($18^{\circ}01'N$ $76^{\circ}48'W$). **Mexico:** Oaxaca, near Ixtlán de Juárez ($17^{\circ}18'48.83''N$ $96^{\circ}28'59.77''W$); near Santiago Comaltepec ($17^{\circ}33'29.63''N$ $93^{\circ}31'55.50''W$). Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Peru:** ($11^{\circ}59'N$ $77^{\circ}03'S$). **Venezuela:** ($10^{\circ}28'N$ $66^{\circ}54'W$).

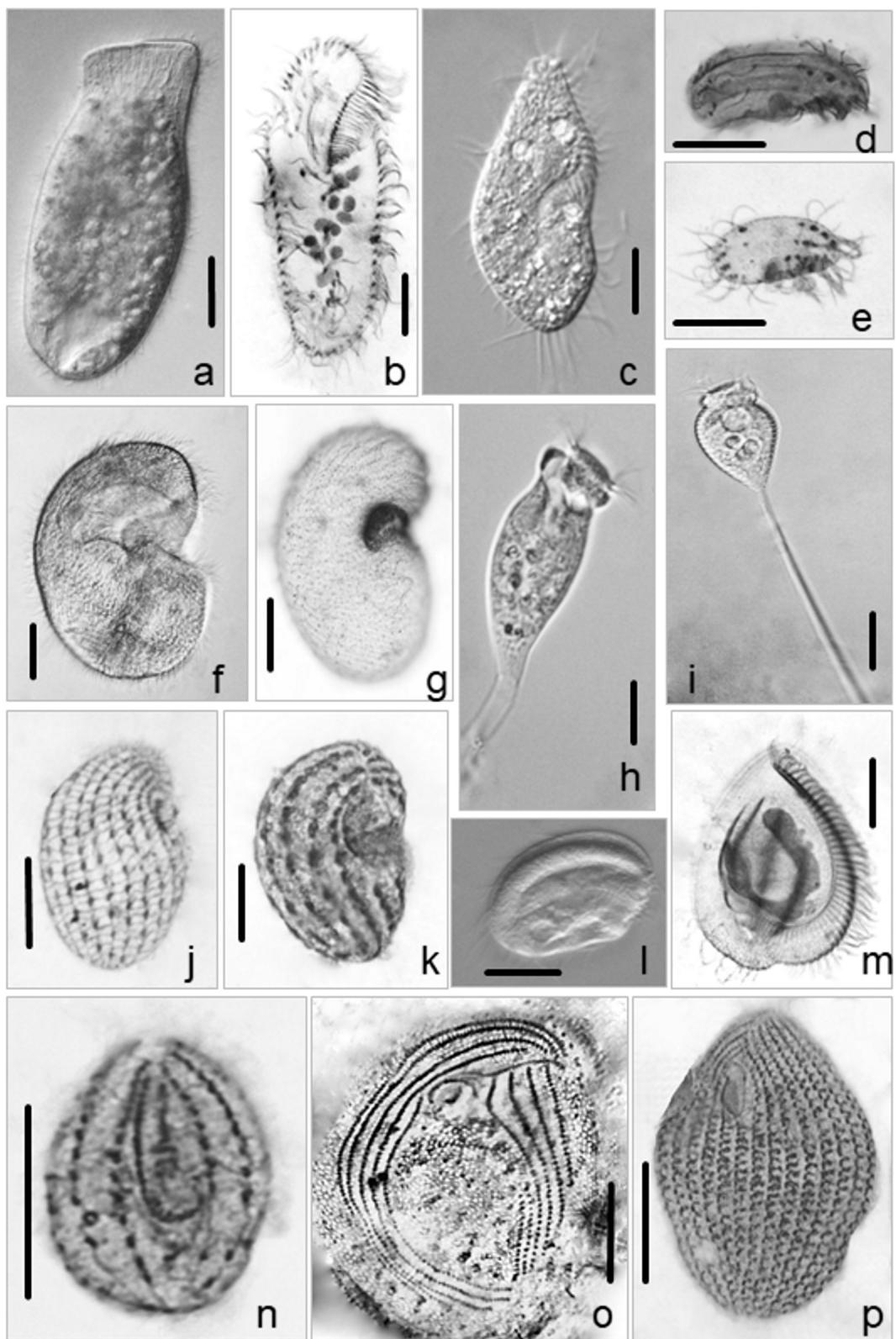


FIGURE 3. a–p. Ciliate from tank-less bromeliads *in vivo* (a, c, f, h, i, l), silver nitrate impregnation (e, j, k, n, o, p), protargol impregnation (b, d, m) and nigrrosine (g). a. *Spathidium spathula*, b. *Pattersoniella vitiphila*, c. *Gonostomum bromelicola*, d. *Drepamomonas revoluta*, e. *D. minuta*, f. *Bresslauides terricola*, g. *Colpoda cucullus*, h. *Epistylis* sp., i. *Vorticella* sp., j. *C. maupasi*, k. *Colpoda aspera*, l. *Leptopharynx costatus*, m. *Phacodinium metchnikoffi*, n. *Cyclidium glaucoma*, o. *Odontochlamys gouraudi*, p. *Tetrahymena* sp. Scale bar: 10 µm. 20 X (f), 40 X (a, b, c, g, h, i, j, l, m, p), 100 X (d, e, k, n, o).

References: Buosi *et al.* 2014; Cruz-Jiménez 2017; Durán-Ramírez *et al.* 2015; Foissner 2010.

Colpoda aspera Kahl, 1926

Kahl, A. 1926. *Arch. Protistenk.* 55: 197–438.

Habitat. Flushs, lithotelmas, moss, swimming pools, tree litter, soil.

Distribution. **Brazil:** Amazonas, outskirts of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$). Bahia, inselbergs within the Atlantic rainforest zone ($16^{\circ}40'13.41''S$ $39^{\circ}09'46.66''W$). **Costa Rica:** Heredia, near Braulio Carrillo National Park ($10^{\circ}12'29.50''N$ $84^{\circ}00'52.25''W$); Puntarenas, near Monteverde Cloud Forest Reserve ($10^{\circ}18'28.07''N$ $84^{\circ}47'48.29''W$). **Ecuador:** Isabela Island at Sierra Negra Crater ($0^{\circ}57'00.59''S$ $90^{\circ}57'31.25''W$). **Mexico:** Morelos, swimming pool in Cuernavaca ($18^{\circ}55'45.14''N$ $99^{\circ}13'58.58''W$); on the road between Yecapixtla and Ocuituco ($18^{\circ}52'29.77''N$ $98^{\circ}51'11.06''W$). Oaxaca, near San Pablo Huitzo ($17^{\circ}15'34.10''N$ $96^{\circ}52'24.42''W$). **Venezuela:** Amazonas, Catanjapo River ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near Fundo El Tesoro ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Falcón, Golfete de Cuare ($10^{\circ}55'26.04''N$ $68^{\circ}17'13.35''W$); Morrocoy National Park ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$); Pico de Chichiriviche ($10^{\circ}54'09.74''N$ $68^{\circ}22'30.47''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$). Mérida, outskirts of Mérida ($8^{\circ}36'52.64''N$ $71^{\circ}09'30.67''W$).

References: Arévalo-Trear 1967; Cruz-Jiménez 2017; Foissner 1997, 2016; Madrazo-Garibay & López-Ochoterena 1982; Steffens & Wilbert 2002.

Colpoda cucullus (Müller, 1773) Gmelin, 1790

Müller, O. F. 1773. Heineck & Faber, Havniae & Lipsiae: [l–30], 1–135.

Habitat. Biological crusts, decaying bark, *Espeletia* leaves, grasslands, guano, flushs, freshwater sponges, moss, ponds, rivers, soil, tank bromeliadas, tree litter.

Distribution. **Argentina:** Buenos Aires, 40 km south of La Plata City ($35^{\circ}23'22.85''S$ $57^{\circ}48'08.79''W$); Buenos Aires City ($34^{\circ}36'23.95''S$ $58^{\circ}22'38.23''W$). Córdoba ($31^{\circ}25'22.17''S$ $64^{\circ}11'14.15''W$). **Brazil:** Amazonas, vicinity of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$). Bahia, inselbergs within the Atlantic rainforest zone ($16^{\circ}40'13.41''S$ $39^{\circ}09'46.66''W$). Minas Gerais, inselbergs within the Atlantic rainforest zone ($19^{\circ}12'40.47''S$ $41^{\circ}17'45.39''W$). Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$). **Colombia:** Leticia, near Leticia town ($4^{\circ}09'51.10''S$ $69^{\circ}58'18.04''W$). **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). Puntarenas, Monteverde Cloud Forest Reserve ($10^{\circ}18'28.07''N$ $84^{\circ}47'48.29''W$). **Ecuador:** Isabela Island ($0^{\circ}57'00.59''S$ $90^{\circ}57'31.25''W$). San Cristóbal Island ($0^{\circ}48'11.41''S$ $89^{\circ}25'59.56''W$). Santa Cruz Island ($0^{\circ}44'20.16''S$ $90^{\circ}18'37.73''W$). **Peru:** Loreto, vicinity of Iquitos ($3^{\circ}46'50.45''S$ $74^{\circ}21'05.75''W$). **Mexico:** Guerrero, La Joya cave ($18^{\circ}35'13.95''N$ $99^{\circ}33'56.76''W$). Morelos, on the road between Yecapixtla and Ocuituco ($18^{\circ}52'29.77''N$ $98^{\circ}51'11.06''W$). Tabasco, grassland near Cunduacán ($18^{\circ}02'42.19''N$ $93^{\circ}09'22.72''W$). Tamaulipas, near Gómez Farías, Rancho El Cielo ($22^{\circ}51'10.80''N$ $99^{\circ}07'19.35''W$). Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); Jalacingo, Ejido Orilla del Monte ($19^{\circ}48'06.88''N$ $97^{\circ}18'16.44''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); Catanjapo River ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near Orinoco River ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); Pavoni ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near Fundo El Tesoro ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$); near Ocumare ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Bolívar, 100 km southwest to Cabruta ($7^{\circ}00'29.36''N$ $66^{\circ}05'48.69''W$); outskirts of Village of Raimundo ($7^{\circ}03'33.83''N$ $66^{\circ}55'39.03''W$). Falcón, Golfete de Cuare ($10^{\circ}55'26.04''N$ $68^{\circ}17'13.35''W$); Morrocoy National Park ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$); Pico de Chichiriviche ($10^{\circ}54'09.74''N$ $68^{\circ}22'30.47''W$). Guárico, near

Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$). Mérida, Cordillera de Mérida ($8^{\circ}52'38.68''N$ $70^{\circ}48'41.56''W$); outskirts of Mérida ($8^{\circ}36'52.64''N$ $71^{\circ}09'30.67''W$); Páramo de Piedras Blancas, near Pico del Águila ($8^{\circ}52'24.71''N$ $70^{\circ}48'31.65''W$).

References: Aladro-Lubel *et al.* 2006; Arévalo-Trear 1967; Bovee 1957; Buosi *et al.* 2014; Durán-Ramírez *et al.* 2015; Foissner 1995, 1997, 2000, 2016; Foissner *et al.* 2003; Küppers & Claps 2012b; Mondragón-Camarillo 2011; Rico-Ferrat 1990; Sigala-Regalado 2011; Steffens & Wilbert 2002.

Colpoda maupasi Enriques, 1908

Enriques, P. 1908. *Arch. Zool. Exp. Gén.* 8: 1–15.

Habitat. Biological crusts, coastal lagoons, decaying bark, guano, mangrove, moss, rivers, soil, tank bromeliads, tree litter.

Distribution. **Brazil:** Amazonas: Janauari Region, 20 km east of Manaus ($3^{\circ}12'53.11''S$ $60^{\circ}02'46.31''W$); Rio Negro, Anavilhanas archipelago ($2^{\circ}38'09.53''S$ $60^{\circ}55'33.53''W$); vicinity of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$). Bahia, inselbergs within the Atlantic rainforest zone ($16^{\circ}40'13.41''S$ $39^{\circ}09'46.66''W$). Minas Gerais, inselbergs within the Atlantic rainforest zone ($19^{\circ}12'40.47''S$ $41^{\circ}17'45.39''W$). **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). Heredia, near Braulio Carrillo National Park ($10^{\circ}12'29.50''N$ $84^{\circ}00'52.25''W$). Puntarenas, Monteverde Cloud Forest Reserve ($10^{\circ}18'28.07''N$ $84^{\circ}47'48.29''W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Ecuador:** Isabela Island, surroundings of the village of Puerto Villamil ($0^{\circ}57'00.59''S$ $90^{\circ}57'31.25''W$); Sierra Negra Crater ($0^{\circ}57'S$ $90^{\circ}57'W$). San Cristóbal Island ($0^{\circ}48'11.41''S$ $89^{\circ}25'59.56''W$). Santa Cruz Island ($0^{\circ}44'20.16''S$ $90^{\circ}18'37.73''W$). **Mexico:** Guerrero, La Joya cave ($18^{\circ}35'13.95''N$ $99^{\circ}33'56.76''W$). Michoacán, Tziranda cave ($19^{\circ}38'23.93''N$ $100^{\circ}30'06.94''W$); Huarimio cave ($18^{\circ}39'44.69''N$ $100^{\circ}53'08.35''W$). Morelos, on the road between Yecapixtla and Ocuituco ($18^{\circ}52'29.77''N$ $98^{\circ}51'11.06''W$). Nayarit, San Blas ($21^{\circ}31'42.67''N$ $105^{\circ}16'49.34''W$). Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); Ixtaczoquitlán, Galicia cave ($18^{\circ}47'04.82''N$ $96^{\circ}59'11.05''W$); Veracruz, temporary lake ($19^{\circ}12'59.52''N$ $96^{\circ}09'56.66''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Peru:** Loreto, vicinity of Iquitos ($3^{\circ}46'50.45''S$ $74^{\circ}21'05.75''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 50 km north of Puerto Ayacucho ($6^{\circ}06'29.45''S$ $67^{\circ}30'07.53''W$); Catanjapo River ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Bolívar, 100 km southwest to Cabruta ($7^{\circ}00'N$ $66^{\circ}05'W$); outskirts of Village of Raimundo ($7^{\circ}03'33.83''N$ $66^{\circ}55'39.03''W$). Falcón, Golfete de Cuare ($10^{\circ}55'26.04''N$ $68^{\circ}17'13.35''W$); Morrocoy National Park, near Chichiriviche ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$); surroundings of the village of Chichiriviche ($10^{\circ}54'09.74''N$ $68^{\circ}22'30.47''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$). Mérida, outskirts of Mérida ($8^{\circ}36'52.64''N$ $71^{\circ}09'30.67''W$).

References: Aladro-Lubel *et al.* 1990; Arévalo-Trear 1967; Durán-Ramírez *et al.* 2015; Foissner 1995, 1997, 2016; Foissner *et al.* 2003; Hernández-Anaya 1981; Sigala-Regalado 2011; Steffens & Wilbert 2002.

Cyclidium glaucoma Müller, 1773

Müller, O. F. 1773. Heineck & Faber, Havniae & Lipsiae: [l–30], 1–135.

Habitat. Coastal lagoons, detritus, lakes, marine, sediments, submerged plants, rivers, soil, tank bromeliads, tree litter.

Distribution. **Argentina:** Buenos Aires, 40 km south of La Plata City ($35^{\circ}23'22.85''S$ $57^{\circ}48'08.79''W$); Poblet ($35^{\circ}04'27.09''S$ $57^{\circ}57'54.05''W$). **Brazil:** Mato Grosso, northern part of the Pantanal ($15^{\circ}36'54.16''S$ $56^{\circ}56'12.85''W$). Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$); upper Paraná river floodplain ($22^{\circ}42'06.63''S$ $53^{\circ}06'09.26''W$). São Paulo, Atibaia river ($23^{\circ}10'27.07''S$ $46^{\circ}39'31.27''W$). **Costa Rica:** Heredia, near Braulio Carrillo National

Park ($10^{\circ}12'29.50''N$ $84^{\circ}00'52.25''W$). **Mexico:** Campeche, Términos lagoon ($18^{\circ}38'19.22''N$ $91^{\circ}45'52.59''W$); Pom lagoon ($18^{\circ}34'21.23''N$ $92^{\circ}08'43.52''W$). Chiapas, Lake Tziscao ($16^{\circ}04'43.22''N$ $91^{\circ}40'39.55''W$). Guerrero, La Joya cave ($18^{\circ}35'13.95''N$ $99^{\circ}33'56.76''W$). Michoacán, Tziranda cave ($19^{\circ}38'23.93''N$ $100^{\circ}30'06.94''W$). Morelos, Cuernavaca, Salto San Antón ($18^{\circ}55'31.22''N$ $99^{\circ}14'34.49''W$). Nayarit, San Blas ($21^{\circ}31'42.67''N$ $105^{\circ}16'49.34''W$). Oaxaca, Lake Analco ($17^{\circ}24'12.36''N$ $96^{\circ}31'45.41''W$); Presa La Azucena ($17^{\circ}05'20.49''N$ $96^{\circ}39'24.58''W$). Tamaulipas, Gómez Farías, Rancho El Cielo ($22^{\circ}51'10.80''N$ $99^{\circ}07'19.35''W$). Veracruz, Boca del Rio ($19^{\circ}05'37.58''N$ $96^{\circ}05'54.99''W$); Alvarado, Mandinga lagoon ($19^{\circ}00'44.95''N$ $96^{\circ}05'49.53''W$); coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); Jalacingo, Ejido Orilla del Monte ($19^{\circ}48'06.88''N$ $97^{\circ}18'16.44''W$); Veracruz, temporary lake ($19^{\circ}13'06.02''N$ $96^{\circ}11'33.34''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Venezuela:** Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$).

References: Aladro-Lubel *et al.* 1990, 2006; Buosi *et al.* 2014; Durán-Ramírez *et al.* 2015; Foissner 1997, 2016; Hardoim & Heckman 1996; Hernández-Anaya 1981; Küppers & Claps 2012b; Madrazo-Garibay & López-Ochoterena 1985; Méndez-Sánchez 2017; Mondragón-Camarillo 2011; Pauleto *et al.* 2009; Rico-Ferrat 1990; Rondello-Bonatti *et al.* 2016; Sigala-Regalado 2011.

Drepanomonas minuta Foissner & Omar, 2014

Omar, A. & Foissner, W. 2014. *Acta Protozool.* 53:295–311.

Habitat. Soil

Distribution. **Ecuador:** Santa Cruz Island ($0^{\circ}44'20.16''S$ $90^{\circ}18'37.73''W$). **Venezuela:** Amazonas, 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$).

References. Foissner 2016.

Drepanomonas revoluta Penard, 1922

Penard, E, 1922. Georg & Cie, Éditeurs. Géneve. 1–331.

Habitat. Biological crusts, decaying bark, flushs, guano, moss, rivers, soil, tank bromeliads, tree litter.

Distribution. **Brazil:** Bahia, inselbergs within the Atlantic rainforest zone ($16^{\circ}40'13.41''S$ $39^{\circ}09'46.66''W$). Mato Grosso, northern part of the Pantanal ($15^{\circ}36'54.16''S$ $56^{\circ}56'12.85''W$). Minas Gerais, inselbergs within the Atlantic rainforest zone ($19^{\circ}12'40.47''S$ $41^{\circ}17'45.39''W$). Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$). Rio de Janeiro, inselbergs within the Atlantic rainforest zone ($22^{\circ}29'25.68''S$ $42^{\circ}52'56.35''W$). **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Mexico:** Guerrero, La Joya cave ($18^{\circ}35'13.95''N$ $99^{\circ}33'56.76''W$). Oaxaca, near Ixtlán de Juárez ($17^{\circ}18'48.83''N$ $96^{\circ}28'59.77''W$); near San Pablo Huitzo ($17^{\circ}15'34.10''N$ $96^{\circ}52'24.42''W$). Veracruz, Ixtaczoquitlán, Galicia cave ($18^{\circ}47'04.82''N$ $96^{\circ}59'11.05''W$); coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Peru:** Loreto, vicinity of Iquitos ($3^{\circ}46'50.45''S$ $74^{\circ}21'05.75''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near Fundo El Tesoro ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$); near Ocumare ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Bolívar, 100 km southwest to Cabruta ($7^{\circ}00'29.36''N$ $66^{\circ}05'48.69''W$). Falcón, about 13 km northwest of the village of Chichiriviche ($11^{\circ}00'07.16''N$ $68^{\circ}23'12.09''W$); Morrocoy National Park, Pico de Chichiriviche ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$).

References. Buosi *et al.* 2014; Cruz-Jiménez 2017; Durán-Ramírez *et al.* 2015; Foissner 1995, 1997, 2016; Foissner *et al.* 2003; Rondello-Bonatti *et al.* 2016; Sigala-Regalado 2011; Steffens & Wilbert 2002.

***Glaucomides bromelicola* Foissner, 2013**

Foissner, W. 2013. *J. Eukaryot. Microbiol.* 60: 137–157.

Habitat. Tank bromeliads.

Distribution. **Chile:** (33°27' S 70°40'W). **Dominican Republic:** Puerto Plata, Botanical Garden (19°48'29.03"N 70°42'42.23"W). **Ecuador:** (0°00' S 78°26'W). **Jamaica:** (18°01'N 76°48'W). **Mexico:** Veracruz, in coffee lands near Coatepec (19°25'02.46"N 96°58'28.02"W); near Xalapa, Santuario del Bosque de Niebla (19°30'56.50"N 96°56'41.65"W). **Peru:** (11°59'N 77°03'S). **Venezuela:** (10°28'N 66°54'W).

References. Durán-Ramírez *et al.* 2015; Foissner 2013.

***Gonostomum bromelicola* Foissner, 2016**

Foissner, W. 2016. *Denisia* 35: 1–912.

Habitat. Tank bromeliads.

Distribution. **Jamaica**, Trelawny (18°15'46.98"N 77°41'59.03"W).

References. Foissner 2016

***Leptopharynx brasiliensis* Foissner & Omar, 2012b**

Omar, A. & Foissner, W. 2012. *Eur. J. Protistol.* 48: 30–47.

Habitat. Soil, tree litter.

Distribution. **Brazil:** Mato Grosso, near Poconé (16°39'28.35"S 56°45'34.55"W). **Venezuela:** Amazonas, 50 km north of Puerto Ayacucho (6°06'29.45"S 67°30'07.53"W); near El Sapo (5°41'33.29"N 67°36'18.70"W).

References. Foissner 2016; Omar & Foissner 2012b.

***Leptopharynx bromelicola* Foissner *et al.*, 2011**

Foissner, Wolf, Yashchenko & Stoeck, 2011. *J. Eukaryot. Microbiol.* 58(2):134–151.

Habitat. Tank bromeliads.

Distribution. **Jamaica:** Slope of the Blue Mountains, Jamaica, Silver Hill village (18°12'01.48"N 76°40'44.46"W). **Mexico:** Oaxaca, near Ixtlán de Juárez (17°18'48.83"N 96°28'59.77"W). Veracruz, in coffee lands near Coatepec (19°25'02.46"N 96°58'28.02"W); near Xalapa, Santuario del Bosque de Niebla (19°30'56.50"N 96°56'41.65"W).

References. Durán-Ramírez *et al.* 2015; Foissner *et al.* 2011.

***Leptopharynx bromeliophilus* Omar & Foissner, 2011**

Omar & Foissner, 2011. *Acta Protozool.* 50:89–103.

Habitat. Tank bromeliads.

Distribution. **Jamaica:** Ecclesdown (18°03'45.09"N 76°20'25.62"W). **Mexico:** Oaxaca, near Ixtlán de Juárez (17°18'48.83"N 96°28'59.77"W). Veracruz, in coffee lands near Coatepec (19°25'02.46"N 96°58'28.02"W); near Xalapa, Santuario del Bosque de Niebla (19°30'56.50"N 96°56'41.65"W).

References. Durán-Ramírez *et al.* 2015; Omar & Foissner 2011.

Leptopharynx costatus Mermod, 1914

Mermod, G. 1914. *Revue Suisse Zool.* 22: 31–114.

Habitat. Biological crusts, decaying bark, *Espeletia* leaves, freshwater sponges, guano, moss, soil, tank bromeliads, tree litter.

Distribution. **Brazil:** Amazonas, Janauari Region, 20 km east of Manaus ($3^{\circ}12'53.11''S$ $60^{\circ}02'46.31''W$); outskirts of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$); Rio Negro, Anavilhanas archipelago ($2^{\circ}38'09.53''S$ $60^{\circ}55'33.53''W$). Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$). **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). Heredia, Braulio Carrillo National Park ($10^{\circ}12'29.50''N$ $84^{\circ}00'52.25''W$). Puntarenas, near Monteverde Cloud Forest Reserve ($10^{\circ}18'28.07''N$ $84^{\circ}47'48.29''W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Ecuador:** ($0^{\circ}00' S$ $78^{\circ}26'W$). **Mexico:** Guerrero: La Joya cave ($18^{\circ}35'13.95''N$ $99^{\circ}33'56.76''W$). Oaxaca, near Ixtlán de Juárez ($17^{\circ}18'48.83''N$ $96^{\circ}28'59.77''W$). Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Peru:** Loreto, vicinity of Iquitos ($3^{\circ}46'50.45''S$ $74^{\circ}21'05.75''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 50 km north of Puerto Ayacucho ($6^{\circ}06'29.45''S$ $67^{\circ}30'07.53''W$); Pavoni ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); near Fundo El Tesoro ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$); near Ocumare ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Bolívar, 100 km southwest to Cabruta ($7^{\circ}00'29.36''N$ $66^{\circ}05'48.69''W$); outskirts of Village of Raimundo ($7^{\circ}03'33.83''N$ $66^{\circ}55'39.03''W$). Falcón, Morrocoy National Park, near Chichiriviche ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$). Mérida, Páramo de Piedras Blancas, near Pico del Águila ($8^{\circ}52'24.71''N$ $70^{\circ}48'31.65''W$).

References. Buosi *et al.* 2014; Durán-Ramírez *et al.* 2015; Foissner 1995, 1997, 2000, 2016; Foissner *et al.* 2003; Sigala-Regalado 2011.

Odontochlamys gouraudii Certes, 1891

Certes, A. 1891. *Mém. Soc. Zool. Fr.* 4: 536–541.

Habitat. Soil, tank bromeliads.

Distribution. **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). **Mexico:** Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 50 km north of Puerto Ayacucho ($6^{\circ}06'29.45''S$ $67^{\circ}30'07.53''W$). Apure, near Fundo El Tesoro ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$).

References. Durán-Ramírez *et al.* 2015; Foissner 1995, 2016.

Paracolpoda steinii (Maupas, 1883)

Maupas, É. 1883. *Archs Zool. Exp. Gen.* (Ser. 2) 11: 427–664.

Habitat. Biological crusts, coastal lagoons, decaying bark, *Espeletia* leaves, flushs, grasslands, lithotelmas, moss, rivers, soil, tank bromeliads, temporary lake, tree litter.

Distribution. **Argentina:** Buenos Aires City ($34^{\circ}36'23.95''S$ $58^{\circ}22'38.23''W$); Poblet ($35^{\circ}04'27.09''S$ $57^{\circ}57'54.05''W$). Córdoba ($31^{\circ}25'22.17''S$ $64^{\circ}11'14.15''W$). **Brazil:** Amazonas, outskirts of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$); Rio Negro, Anavilhanas archipelago ($2^{\circ}38'09.53''S$ $60^{\circ}55'33.53''W$). Bahia, inselbergs within the Atlantic rainforest zone ($16^{\circ}40'13.41''S$ $39^{\circ}09'46.66''W$). Minas Gerais, inselbergs within the Atlantic rainforest zone ($19^{\circ}12'40.47''S$ $41^{\circ}17'45.39''W$). Rio de Janeiro, inselbergs within the Atlantic rainforest zone ($22^{\circ}29'25.68''S$ $42^{\circ}52'56.35''W$). Paraná, Nupélia Field Station near Porto São José

($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$); upper Paraná river floodplain ($22^{\circ}42'06.63''S$ $53^{\circ}06'09.26''W$). São Paulo, inselbergs within the Atlantic rainforest zone ($23^{\circ}11'08.32''S$ $45^{\circ}01'27.49''W$). **Costa Rica:** Heredia, near Braulio Carrillo National Park ($10^{\circ}12'29.50''N$ $84^{\circ}00'52.25''W$); Puntarenas, near Monteverde Cloud Forest Reserve ($10^{\circ}18'28.07''N$ $84^{\circ}47'48.29''W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Ecuador:** ($0^{\circ}00'S$ $78^{\circ}26'W$). Isabela Island at Sierra Negra Crater ($0^{\circ}57'00.59''S$ $90^{\circ}57'31.25''W$). Isabela Island, surroundings of the village of Puerto Villamil ($0^{\circ}57'00.59''S$ $90^{\circ}57'31.25''W$). San Cristóbal Island ($0^{\circ}48'11.41''S$ $89^{\circ}25'59.56''W$). Santa Cruz Island ($0^{\circ}44'20.16''S$ $90^{\circ}18'37.73''W$). **Mexico:** Nayarit, San Blas ($21^{\circ}31'42.67''N$ $105^{\circ}16'49.34''W$). Tamaulipas, Gómez Farías, Rancho El Cielo ($22^{\circ}51'10.80''N$ $99^{\circ}07'19.35''W$). Veracruz, in coffee lands near Coatepec ($19^{\circ}25'02.46''N$ $96^{\circ}58'28.02''W$); Jalacingo, Ejido Orilla del Monte ($19^{\circ}48'06.88''N$ $97^{\circ}18'16.44''W$); Veracruz, temporary lake ($19^{\circ}13'06.02''N$ $96^{\circ}11'33.34''W$); near Xalapa, Santuario del Bosque de Niebla ($19^{\circ}30'56.50''N$ $96^{\circ}56'41.65''W$). **Peru:** Loreto, vicinity of Iquitos ($3^{\circ}46'50.45''S$ $74^{\circ}21'05.75''W$). **Venezuela:** Amazonas: 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); 14 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$); Pavoni ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Apure: near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Bolívar, 100 km southwest to Cabruta ($7^{\circ}00'29.36''N$ $66^{\circ}05'48.69''W$); outskirts of Village of Raimundo ($7^{\circ}03'33.83''N$ $66^{\circ}55'39.03''W$). Falcón, about 13 km northwest of the village of Chichiriviche ($11^{\circ}00'07.16''N$ $68^{\circ}23'12.09''W$); Golfete de Cuare ($10^{\circ}55'26.04''N$ $68^{\circ}17'13.35''W$); Morrocoy National Park, near Chichiriviche ($10^{\circ}55'44.17''N$ $69^{\circ}19'44.72''W$); Pico de Chichiriviche ($10^{\circ}54'09.74''N$ $68^{\circ}22'30.47''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$). Mérida, outskirts of Mérida ($8^{\circ}36'52.64''N$ $71^{\circ}09'30.67''W$); Páramo de Piedras Blancas, near Pico del Águila ($8^{\circ}52'24.71''N$ $70^{\circ}48'31.65''W$); Sierra Nevada National Park, surroundings of La Mucuy ($8^{\circ}37'55.79''N$ $71^{\circ}02'12.20''W$).

References. Aladro-Lubel *et al.* 1990; Buosi *et al.* 2014; Foissner 1997, 2000, 2016; Foissner *et al.* 2003; Durán-Ramírez *et al.* 2015; Hernández-Anaya 1981; Küppers & Claps 2012a, 2016; Mondragón-Camarillo 2011; Pauleto *et al.* 2009; Rico-Ferrat 1990; Steffens & Wilbert 2002.

***Pattersoniella vitiphila* Foissner, 1987b**

Foissner, W. 1987b. *Zool. Beitr. N. F.* 31(2):187–282.

Habitat. Alluvial soil, soil, tank bromeliads.

Distribution. **Brazil:** Paraná, Nupélia Field Station near Porto São José ($22^{\circ}45'04.27''S$ $53^{\circ}15'43.82''W$); São Pedro do Paraná ($22^{\circ}43'16.90''S$ $53^{\circ}10'10.85''W$). **Dominican Republic:** ($18^{\circ}28'N$ $69^{\circ}56'W$). **Venezuela:** Aragua, Henri Pittier National Park ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$).

References. Buosi *et al.* 2014; Foissner 2016; Foissner *et al.* 2003.

***Phacodinium metchnikoffi* (Certes, 1891) Prowazek, 1900**

Certes, A. 1891. *Mém. Soc. Zool. Fr.* 4: 536–541.

Habitat. Moss, soil.

Distribution. **Brazil:** Rio Negro, Anavilhanas archipelago ($2^{\circ}38'09.53''S$ $60^{\circ}55'33.53''W$). **Mexico:** Oaxaca, near San Pablo Huitzo ($17^{\circ}15'34.10''N$ $96^{\circ}52'24.42''W$). **Venezuela:** Apure, near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$); near Ocumare ($10^{\circ}30'00.05''N$ $67^{\circ}37'33.64''W$). Guárico, near Cabruta ($7^{\circ}38'49.83''N$ $66^{\circ}14'10.58''W$).

References. Cruz-Jiménez 2017; Foissner 1997, 2016.

***Spathidium spathula* (Müller, 1773) Bütschli, 1889**

Müller, O. F. 1773. Heineck & Faber, Havniae & Lipsiae: [l–30], 1–135.

Habitat. Pools, soil.

Distribution. **Argentina:** Buenos Aires City ($34^{\circ}36'23.95''S$ $58^{\circ}22'38.23''W$). **Brazil:** Amazonas, outskirts of Manaus ($3^{\circ}09'16.94''S$ $60^{\circ}16'16.76''W$). **Costa Rica:** Guanacaste, Santa Rosa National Park ($10^{\circ}49'49.79''N$ $85^{\circ}42'42.64''W$). **Venezuela:** Amazonas, 10 km north of Puerto Ayacucho ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Apure, near El Sapo ($5^{\circ}41'33.29''N$ $67^{\circ}36'18.70''W$). Aragua, Biological Station Rancho Grande ($10^{\circ}23'20.36''N$ $67^{\circ}37'07.85''W$).

References. Foissner 1995, 1997, 2016; Küppers & Claps 2012a.

Discussion

Previous studies about ciliate communities from bromeliads have been carried out only from species with tank morphology. Our results provide evidence that other species, and even other genera of tropical tank-less bromeliads, with a similar vegetative architecture to *Espeletia* from the Andean paramos (Foissner 2000), constitute a habitat for ciliates. Ciliate species richness recorded from a tank-less bromeliad species like *T. dasyliriifolia* was lower in comparison with tank bromeliads like the *Tillandsia biflora* complex from a montane cloud forest in Central Mexico (Durán-Ramírez *et al.* 2015), or *Aechmea distichantha* from a tropical subdeciduous forest in South Brazil (Buosi *et al.* 2014), which contained double and triple species richness respectively. In addition to the bromeliad morphology, the type of forest might be influencing the ciliate species composition in bromeliads. In the case of terrestrial bromeliads like *B. karatas* and *B. pinguin*, their proximity to the ground can be an important factor that allows colonization of soil ciliates like colpodids and spirotricheans, which were the most common ciliates in our samples.

The dry season in the RBCC lasts two thirds of the year. For this reason, terrestrial and epiphytic bromeliads could be acting as cysts reservoirs when environmental conditions like humidity degree are not suitable for ciliates. An outstanding observation was the record of the hymenostomatid *Glaucomides bromelicola* from *T. rothii*, which was one of the eight bromeliads where dry detritus and no water were collected due to the absence of precipitation the days before sampling. The cysts of this ciliate species has not been described yet, and Foissner (2013) established that *G. bromelicola* does not have the ability to produce this type of resistance phase of its life cycle when the bromeliad tank desiccates. However, its presence after rehydration of dry detritus, could be considered as indirect evidence that under unknown circumstances, *G. bromelicola* is able to encyst while waiting for more favorable conditions.

In the context of geographical distribution of ciliates in the Neotropics, we found that studies of alpha-diversity are scarce for this biogeographical region, and some countries in the Neotropics did not have any records. Of the total number of taxa identified at species level, 13 species showed a cosmopolitan distribution and six have a geographical distribution restricted to the Neotropics. Concerning bromeliads, in spite of their wide distribution in different Neotropical ecosystems, detailed studies about ciliates and bromeliads have been conducted only in few countries such as Brazil. For example, the gonostomatid *Gonostomum bromelicola* has only been recorded from its type locality (Foissner 2016), and for this reason, it has been considered a Gondwanan endemic species. Its presence in bromeliads from RBCC, supports the moderate endemicity model of Foissner (2008); however, the idea of a wider distribution on ciliates according to the geological evolution and split of Gondwanna and Laurasia can also be considered (Bourland 2017). Another example is the oxytrichid *Pattersoniella vitiphila*, a species only known from few localities in the Southern Hemisphere (Berger 1999), which has been recently observed in the Northern Hemisphere.

According to previous records, soil is the most common habitat of the ciliates species found in this study. Other common habitats in the Neotropics for this group of species include rivers, decaying bark, tank bromeliads, moss, tree litter, and biological crusts. In the case of ciliates that show specificity to inhabit bromeliads, both tank and tank-less, their geographical distribution matches the distribution of family Bromeliaceae. However, the existence of different distributional patterns of a single ciliate species or group of species within the Neotropical region is unknown. Our results represent the first records of ciliates in tank-less bromeliads and contribute to the knowledge about the biodiversity of the RBCC and the dry tropical forest, as well as to the general knowledge about ciliates that inhabit bromeliads in the Neotropics.

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Capítulo II

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Ciliate community structure in bromeliads of different types of vegetation in eastern Mexico.

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Ciliate Community Structure in Bromeliads of Different Types of Vegetation in Eastern Mexico

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Abstract. To understand distributional and ecological aspects of ciliates living in tank bromeliads, we analyzed the ciliate community structure in fifteen different epiphytic and terrestrial bromeliad species from different types of vegetation. Sixty-nine samples were collected from plants of genera *Aechmea*, *Bromelia*, *Pseudalcantarea* and *Tillandsia* in seven localities in eastern Mexico during 2014 and 2015. The sampling localities covered an altitude gradient from 0 till 2 210 m ASL. We found 24 ciliate species and through the application of a principal component analysis, three clusters that correspond to several types of vegetation were obtained with regard to ciliate and bromeliad species. We recorded the largest number of ciliate species in localities of montane cloud forest, and also the largest number of ciliate species endemic to tank bromeliads, like *Glaucomides bromelicola*, inhabiting bromeliads from this forest. We observed the presence of ciliates in *Bromelia pinguin* that possesses a weakly developed phytotelm. The results of our study indicate that the species composition of ciliates inhabiting tank bromeliads depends on such correlated environmental factors like altitude ASL, temperature and type of vegetation.

Keywords: Neotropics, phytotelma, ciliates.

INTRODUCTION

Global diversity of ciliates still remains unknown, with at least a half of their estimated diversity undescribed. The lack of studies in many terrestrial, marine and limnetic ecosystems is one of the reasons that dis-

tributional patterns of ciliates at global and local scale remains strongly debated between protistologist (Foissner 1999, 2006).

Ciliates play an important role by grazing on bacterial populations in a wide variety of ecosystems, participating in nutrient cycling, and contributing in a significant way to the so called terrestrial microbial loop (Fenchel 1980, Clarholm 1985, Pomeroy et al. 2007). Studies of ciliate diversity from tank bromeliads are scarce and have been mainly carried out with a taxonomic focus (Foissner et al. 2003, Dunthorn et al. 2012, Durán-Ramírez and Mayén-Estrada 2018,

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Durán-Ramírez et al. 2015). Many aspects of the ecology and distribution of bromeliad-associated ciliates in the Neotropics are almost unknown. Recently, Buosi et al. (2014, 2015) documented the importance of water to the establishment of ciliates in bromeliads where seasonality influenced their abundances, but they found no evidence of a spatial effect between plants at population level. Impoundments of water in tank bromeliads represent an ideal model to study ciliate ecology and their distributional patterns in Neotropical forests. For this reason, the distribution of ciliates in tank bromeliads at local scale and their community structure, can be elucidated through the comparison of different types of vegetation where bromeliads occur.

Many bromeliad species are so-called “tank bromeliads”, that collect water in a central “tank” formed by the rosette of leaves and often in peripheral collections formed by leaf axils (Benzig 2000). Nadkarni (1994) considered tank bromeliads as keystone resources in the forest and the water impoundments that they form microecosystems termed “phytotelmata” (Maguire 1971).

The ciliate communities inhabiting the water of tank bromeliads, are composed of some species that show a cosmopolitan distribution and others are that considered as endemics to bromeliads (Foissner et al. 2003, Durán-Ramírez et al. 2015). Host specificity between ciliate species and bromeliads has not yet been demonstrated (Foissner et al. 2003).

The state of Veracruz, in eastern Mexico, shows a wide variety of types of vegetation and floristic richness (Rzedowski 1978) where almost one hundred species of bromeliad have been recorded (Espejo-Serna et al. 2005). The objective of our study was to analyze the free living ciliate community structure in different epiphytic and terrestrial tank bromeliad species, inhabiting in different types of vegetation in eastern Mexico. Our results contribute to the knowledge about ciliate diversity, ecology and biogeography, in bromeliad phytotelmata of the Neotropics.

MATERIALS AND METHODS

Area of study. We collected samples during December 2014, April and May of 2015 from seven localities in the state of Veracruz, eastern Mexico (Fig. 1), including a fragment of semideciduous tropical forest on coastal dunes along the coastal shore with only one locality; two localities with remnants of semideciduous tropical forest; two coffee plantations (one with remnants of semideciduous tropical forest and the other with remnants of montane cloud forest); a fragment of montane cloud forest, and also an ecotone between

the montane cloud forest and pine forest; all localities included fragments of forest with some degree of perturbation, surrounded by urban and agricultural zones. Localities belong to the municipalities of Acajete (locality 1), Xalapa (locality 2), Coatepec (locality 3), Jalcomulco (locality 4), Tuzamapan (locality 5), and Actopan (localities 6 and 7) (Fig. 1, Table 1). Localities did not show a continuous forest cover, due to the high level of fragmentation, this affected the number of samples collected and distances separating neighbor localities.

Sample collection. We collected 69 samples of water with detritus in the rosettes of 15 bromeliad species of genera *Aechmea* Ruiz and Pav. 1793, *Bromelia* L. 1753, *Pseudalcantarea* (Mez) Pinzón and Barfuss, 2016 and *Tillandsia* L. 1753, with regard to their impoundment capacity and degree of development of the phytotelmata according to Benzig (2000). In each locality we collected five to 22 samples from different bromeliads depending on their availability (Table 1). We only collected samples from native terrestrial or epiphytic bromeliad species. Epiphytic plants were located about 1.5 m above ground. All plants contained water in their tanks and were separated from each other by a minimum distance of five meters. Samples of water and detritus were collected with new plastic pipettes and placed into sterilized Falcon tubes. The water temperature impounded inside the tank was measured using a thermometer (Taylor-5984). None of the plants were removed from their habitat. The bromeliads were photographed, and water samples maintained at room temperature.

Ciliate identification. To carry out taxonomical identification of ciliates, we analyzed each one of the 69 samples 48 hours after they were collected and at intervals of two days through the next two weeks. We established cultures in Petri dishes using some drops of the original sample, table water Evian®, and wheat grains to stimulate bacterial growth (Foissner et al. 2003). We observed cytological characters of taxonomical importance *in vivo* (e.g. cell size and shape, position and shape of the cytostome, position and number of the contractile vacuoles) using bright field and differential interference contrast microscopy with a Nikon Labophot-2 microscope equipped with a Nikon Digital Sight DS-L15667 camera. We performed silver impregnation techniques according to the protocols of Foissner (2014), to reveal oral and somatic infraciliature, number and disposition of cirri, the silverline pattern, and nuclear apparatus. Microphotographs of some ciliates identified were taken with a Photo Microscope Olympus-Provis AX70 and Evolution MP5 megapix camera. We followed Czapik (1968), Curds (1975), Lee et al. (1985), Dragesco and Dragesco-Kernéis (1986), Foissner (1993, 2003, 2010, 2013), Foissner et al. (1991, 2011), Borror and Hill (1995), Berger (1999, 2006), Foissner and Stoeck (2011), Omar and Foissner (2011, 2013), and Fan et al. (2013) for species identification. Systematics is according to Lynn (2008).

Analysis of community structure. For the data analysis, we evaluated the similarity between localities and performed a Jaccard index analysis ($IJ_{A,B} = c/[a+b-c]$), where a is the number of species in the locality A , b is the number of species in the locality B , and c is the number of species shared between A and B , using a grouping analysis based on the UPGMA algorithm for presence/absence data (Moreno 2001; MVSP 3.22 Kovach Computing Services). Through a principal component analysis (PCA) we evaluated the association between a) the ciliate community structure and biotic factors like bromeliad species, and b) type of vegetation and abiotic factors like water temperature and altitude for each locality. For

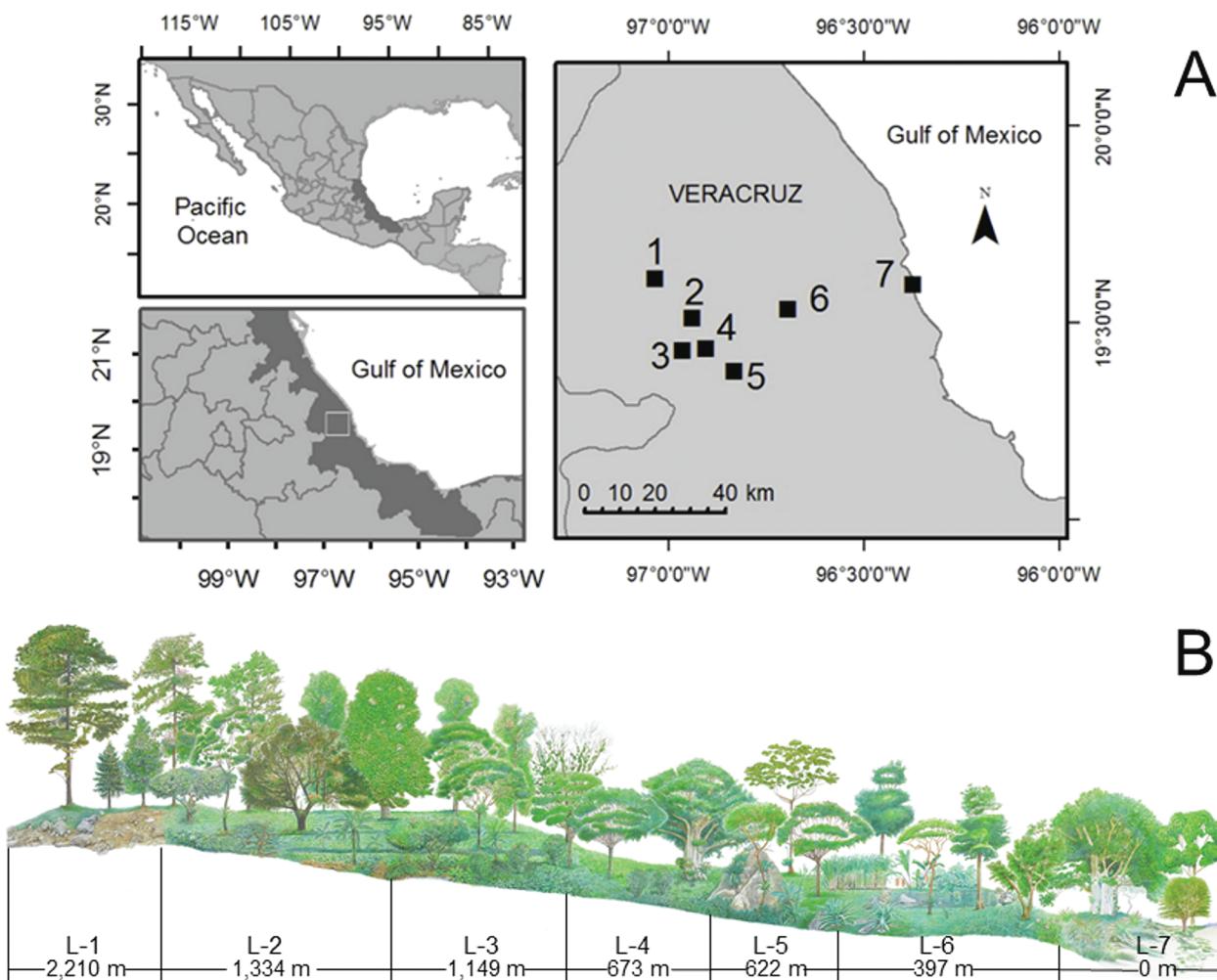


Fig. 1. A. Location of the seven localities of the study. B. Schematic representation of the vegetation from the mountain region to the seashore in east Veracruz, Mexico. L = locality, 1 = La Joya, Acajete; 2 = Santuario de Bosque de Niebla, Xalapa; 3 = Coffee plantation La Onza, Coatepec; 4 = Coffee plantation Arcos Vegas y Rincón de Yeguas, Tuzamapan; 5 = Tlacuitlapa, Jalcomulco; 6 = Unidad de Manejo Ambiental Nace El Río, Descabezadero, Actopan; 7 = Centro de Investigaciones Costeras La Mancha (CICOLMA), Actopan.

categorical variables, we assigned numerical values to include them into the analysis. To carry out the PCA, we applied the PRINCOMP procedure by using the statistical software package SAS University (SAS Institute, Cary, NC, U.S.A.). All graphics were plotted using the statistical software Prism 7.0 (Graph Pad Software, La Joya, CA, U.S.A.).

The five types of vegetation and agroecosystems were coded with values from 0 to 4, where 0 = semideciduous tropical forest, 1 = coffee plantation with remnants of semideciduous tropical forest, 2 = coffee plantation with remnants of montane cloud forest, 3 = montane cloud forest, and 4 = ecotone of montane cloud forest and pine forest. Bromeliad names were coded by using a number for each species according to their distribution in the localities.

RESULTS

Ciliate richness. The 69 bromeliads sampled belonged to 15 species of genera *Aechmea*, *Bromelia*, *Pseudalcantarea* and *Tillandsia* (Table 1). Mean values of water temperature impoundments are shown in Table 1 and Fig. 2. We found a total of 24 ciliate species, grouped in 17 genera (Tables 2–3, Fig. 4). The order Microthoracida showed the largest species richness, and *Leptopharynx* was the genus with most species (four). We recorded *Glaucomides bromelicola* (Fig. 4j) as the most frequent species present in 33 samples, and in 12 of the 15 bromeliad species. In contrast, nine

Table 1. Environmental data and ciliate species richness in the localities.

Locality	Vegetation type	Altitude (m ASL)	n	ATW (°C)	Bromeliad species
1	PF	2,210	10	12	T2 (e-IV), Tm (e-IV), Ty (e-IV)
2	MCF	1,334	22	17.6	Td (e-IV), Ts (e-IV), Tu (e-IV), Pv (e-IV)
3	C-MCF	1,149	10	16.7	Th (e-IV), Ti (e-IV)
4	C-MCF	673	5	20.6	Ab (e, t-III), Am (t-III)
5	SDTF	622	7	21	Pg (t-IV), T1(e-IV), Ab (e-III)
6	SDTF	397	5	20.4	Pg (t-IV), Ab (e-III)
7	SDTF	0	10	22.9	Tc (e-V), Bp (t-I)

Abbreviations of bromeliad species: Ab = *Aechmea bracteata*, Am = *Aechmea mexicana*, Bp = *Bromelia pinguin*, Pg = *Pseudalcantarea grandis*, Pv = *Pseudalcantarea viridiflora*, Tc = *Tillandsia concolor*, Td = *Tillandsia deppeana*, Th = *Tillandsia heterophylla*, Ti = *Tillandsia limbata*, Tm = *Tillandsia macrochlamys*, Tu = *Tillandsia multicaulis*, Ts = *Tillandsia* sp., Ty = *Tillandsia gymnobotrya*, T1 = *Tillandsia* sp.1, T2 = *Tillandsia* sp.2, e = epiphyte, t = terrestrial, I-V = ecological type according to Benzig (2000), ATW = Average temperature of water, SDTF = Semideciduous tropical forest, C = Coffee plantation, MCF = Montane cloud forest, PF = *Pinus* forest, n = number of collected samples.

Table 2. Records based on presence – absence of ciliate species from bromeliads in the localities.

Ciliate species	T. H.	L1	L2	L3	L4	L5	L6	L7
<i>Anteholosticha</i> sp.		+						
<i>Bromeliophrya brasiliensis</i> Foissner, 2003*	B		+	+				
<i>Bromeliothrix metopoides</i> Foissner, 2011	B		+	+	+		+	+
<i>Chilodonella uncinata</i> (Ehrenberg, 1838)	S, T		+	+	+		+	
<i>Colpoda cucullus</i> (Müller, 1773)	S, T	+	+	+			+	+
<i>Colpoda maupasi</i> Enriques, 1908	S, T		+	+		+	+	+
<i>Cotterillia bromelicola</i> Foissner & Stoeck, 2011	B	+	+					
<i>Drepanomonas revoluta</i> Penard, 1922	S, T		+	+				
<i>Euplotopsis</i> sp.								+
<i>Frontonia pusilla</i> Fan <i>et al.</i> , 2013*	M							+
<i>Glaucomides bromelicola</i> Foissner, 2013	B	+	+	+	+	+	+	
<i>Halteria</i> spp.		+	+	+			+	+
<i>Lambornella</i> spp.		+	+	+	+	+	+	
<i>Leptopharynx australiensis</i> Omar & Foissner, 2011*	T							+
<i>Leptopharynx bromelicola</i> Foissner <i>et al.</i> , 2011	B		+					
<i>Leptopharynx bromeliophilus</i> Omar & Foissner, 2011	B	+	+	+				
<i>Leptopharynx</i> spp.		+	+	+			+	
<i>Oxytricha</i> sp.								+
<i>Paracolpoda steinii</i> (Maupas, 1883)	S, T			+				+
<i>Peritrichia</i> 1			+					
<i>Peritrichia</i> 2							+	
<i>Peritrichia telotroch</i>								+
<i>Tetrahymena</i> spp.			+	+		+		
<i>Vorticella</i> sp.								+
Total of species per locality	9	15	12	4	5	7	11	

*New record in Mexico.

T.H. = Type of habitat of previous records: B = bromeliads, S = semiterrestrial, T = terrestrial, M = mangrove.

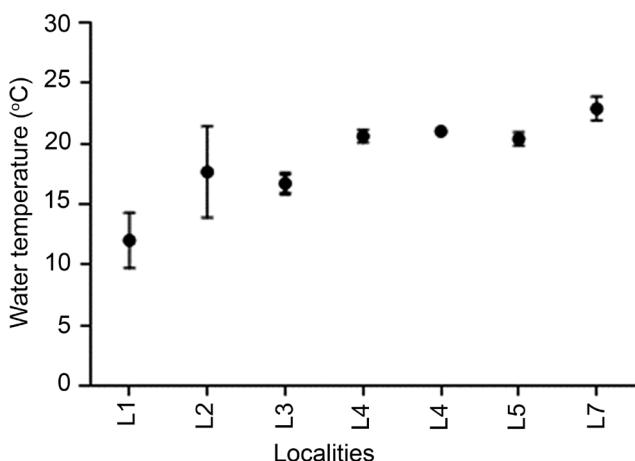


Fig. 2. Average of water temperature of the samples in relation to the localities were samples were collected. Bars indicate standard deviation.

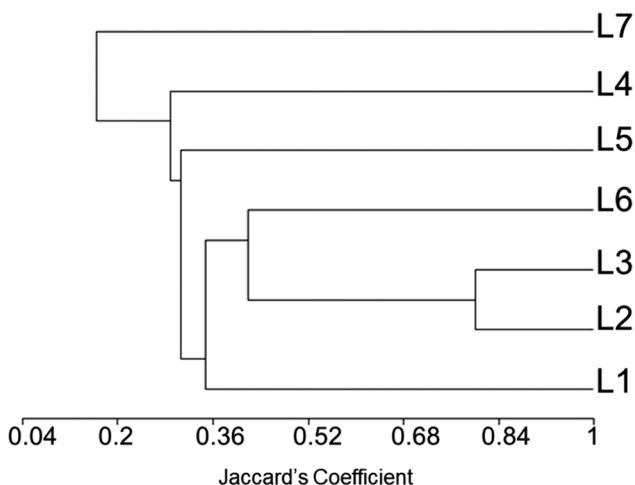


Fig. 3. Dendrogram of the Jaccard's similarities among localities based on the unweighted pair-group method analysis (UPGMA). For the name of the localities see table 1.

ciliate species were observed only from a single bromeliad species (Tables 2–3). *Lambornella* spp. (Fig. 4h) were observed in almost all the localities with exception to locality 7. None of the ciliate species was present in all the 69 samples. The mean number of ciliate species was 9.1 per locality, and 2.8 per plant. Each ciliate species was recorded in seven samples on average (Table 2). Eleven species were only present in one or two samples. Ciliates were not detected in 20 percent of the samples.

Ciliate community structure according to localities. Ciliate community structure was different between localities. We found that locality 2 showed

the highest richness with 15 species in the fragment of montane cloud forest in *Pseudalcantarea viridiflora*, *Tillandsia deppeana*, *T. multicaulis*, and *Tillandsia* sp., followed by localities 3 and 7 with 12 and 11 ciliate species respectively. Epiphytic bromeliads of the pine forest in locality 1 showed nine species, locality 6 seven species, locality 5 five species, and locality 4 had the lowest number of species, four species in *Aechmea bracteata* and *A. mexicana* (Table 2).

From localities 2 to 6 we observed most of the species that are considered endemics of tank bromeliads, i.e. *Bromeliophrya brasiliensis*, *Bromeliothrix metopoides*, *Leptopharynx bromelicola*, *L. bromeliophilus* and *Glaucomides bromelicola*. With the Jaccard similarity analysis, we obtained a maximum similarity value of 0.80 between localities 2 and 3, which corresponded to fragment of montane cloud forest, and the coffee plantation with remnants of this type of forest. The rest of localities showed similarity values < 0.5 (Fig. 3).

The PCA evaluated the association between ciliate community structure related to biotic (bromeliad species and type of vegetation) and abiotic factors (water temperature and elevation) considered in the study. Three principal components were retained and explained together 94.65 percent of the total variation within the data set. The first component explained 62.94 percent of the total variation, and showed a relation between biotic and abiotic factors, where the type of vegetation, bromeliad identity and elevation showed high positive loads to the first axis of variation. In contrast, water temperature showed high loads but was negatively related to the same axis. The second eigenvector only showed high positive loads for ciliate richness in each sample, being the second principal component that showed the ciliate community structure (Fig. 5A). Figure 5B showed that water temperature and type of vegetation were positively related with high loads to the third principal component, unlike ciliate community structure and elevation because of their low and negative correlation to this component. The scores of principal components 1 and 2 for the localities (Fig. 5B), and the type of vegetation and ciliate community structure (Fig. 5C), showed the association pattern between variables and components. In addition to the observed pattern of point dispersal (Fig. 5B), the three clustered groups correspond to each one of the types of vegetation, and entailed their separation from the axis 1 (Fig. 5C).

Semideciduous tropical and pine forest are clearly separated from montane cloud forest and coffee lands

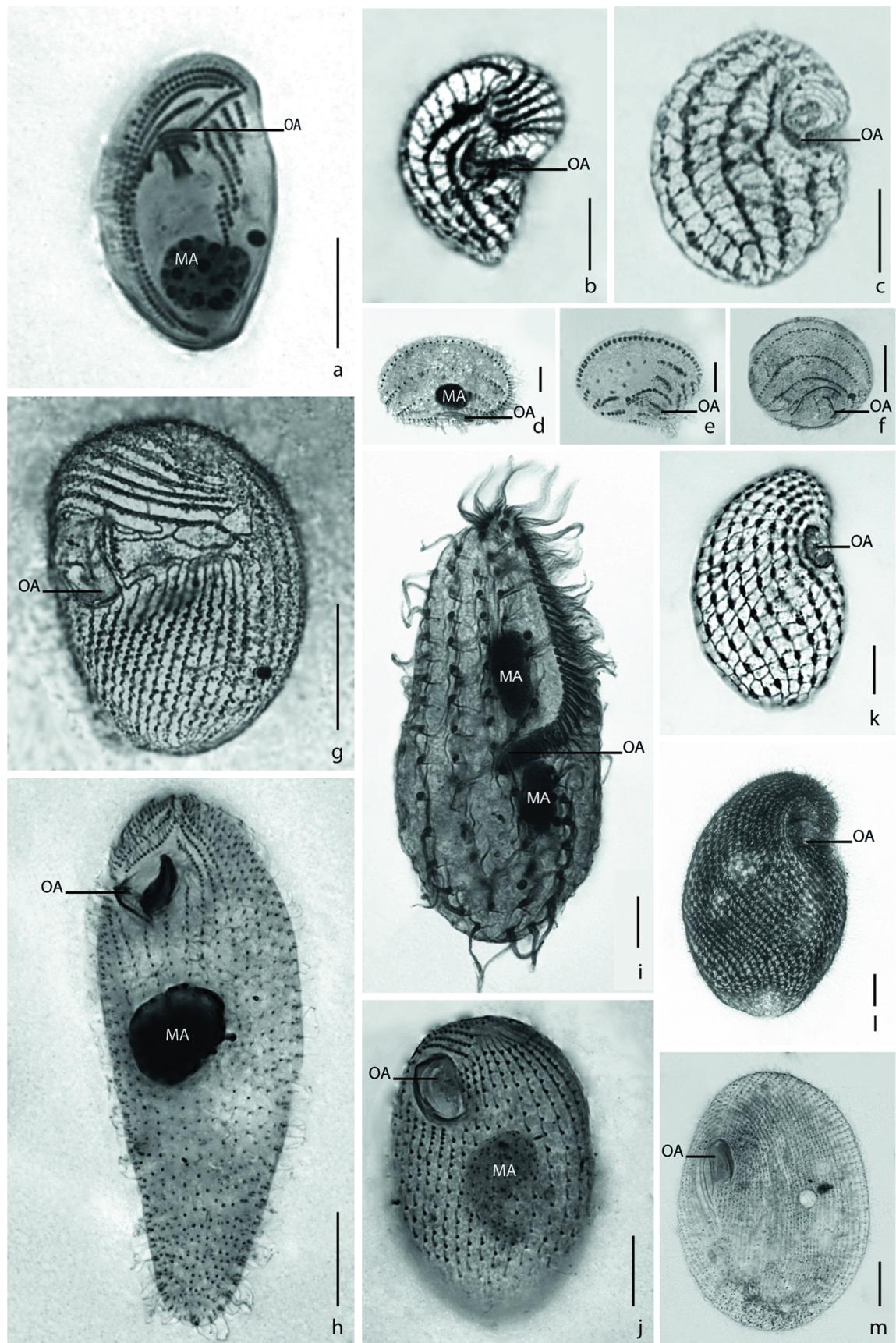


Fig. 4. Ciliates from the tank bromeliads after dry silver nitrate impregnation (b–c, e–g, k–m), and after protargol method (a, d, h–l). a. *Chilodonella uncinata*, b. *Bromeliothrix metopoides*, c. *Paracolpoda steinii*, d. *Leptopharynx australiensis*, e. *L. bromeliophilus*, f. *L. bromelicola*, g. *Bromeliophrya brasiliensis*, h. *Lambornella* sp., i. *Cotterillia bromelicola*, j. *Glaucomides bromelicola*, k. *Colpoda maupasi*, l. *C. cucullus*, m. *Frontonia pusilla*. MA: macronucleus, OA: oral apparatus. Scale bars: 10 µm.

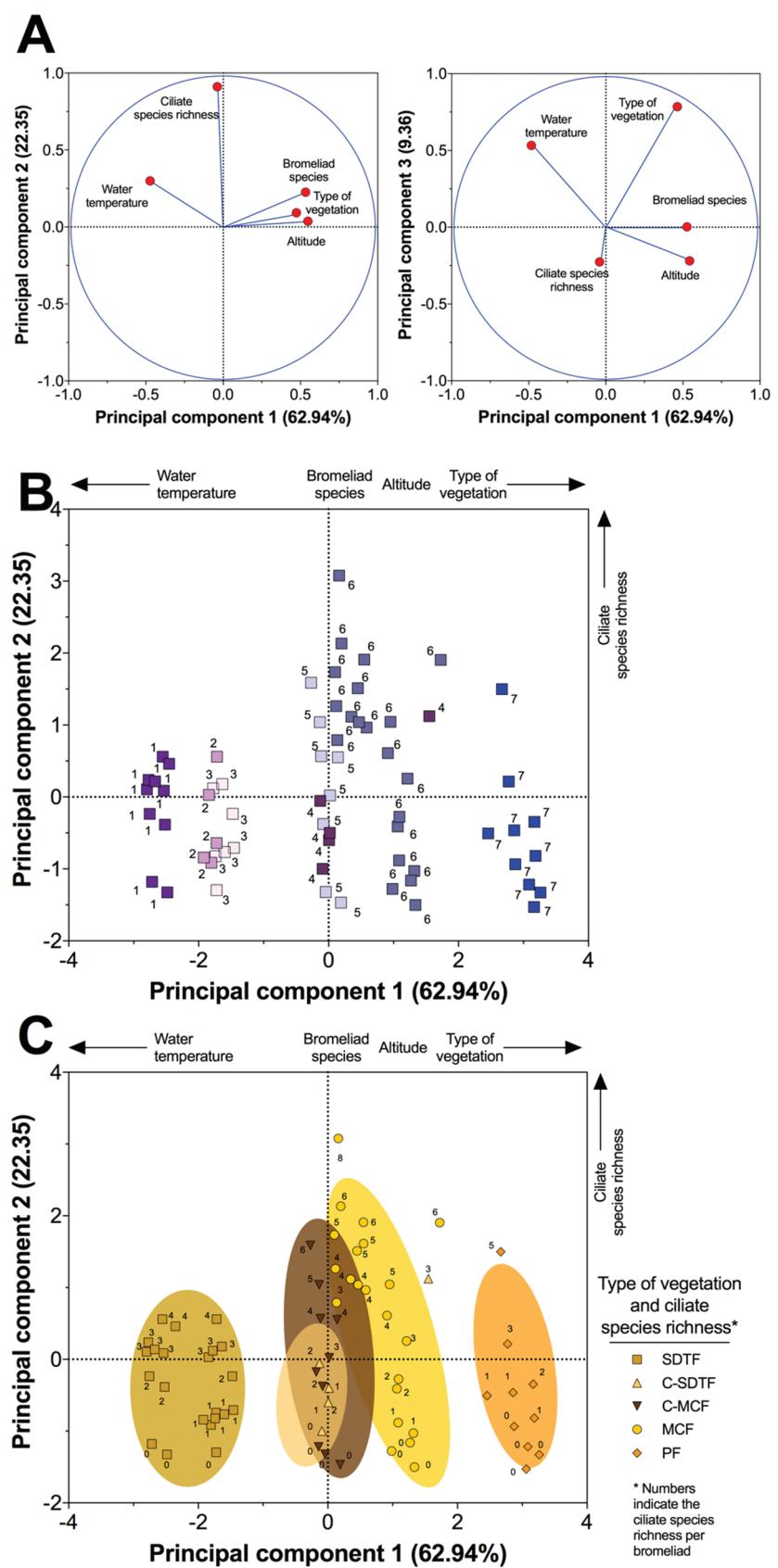


Fig. 5. A. Trait loadings of retained components in the PCA axes 1 and 2, (B) for each sampling carried out in the seven localities, and (C) for vegetation type and ciliate species richness according to the principal components of model A, of an ordination based on species richness, two continuous and two categorical functional traits of 24 ciliate species at Eastern Veracruz, Mexico. Model C shows prediction ellipses at 95% confidence interval to delimitate the vegetation types. Numbers in B refer to the localities. SDTF = Semideciduous tropical forest, C = Coffee plantation, MCF = Montane cloud forest, PF = *Pinus* forest.

showed the higher ciliate species richness. Each one of the sampled bromeliads and their respective number of ciliate species were represented by the set of points that are distributed in the axis 2 (Fig. 5C). The bromeliads with a larger ciliate species richness showed higher positive scores in axis 2.

DISCUSSION

Ciliate species composition, geographical distribution and their ecological aspects in tank bromeliads remain poorly understood. Our results indicate that ciliate species composition in bromeliads have local patterns of geographical distribution in relation to the type of vegetation in this part of the Neotropics. We found that species richness was larger at the montane cloud forest and ciliate communities have different species composition.

Due to the absence of specificity between ciliates-bromeliads, we did not consider the plant identity for the sampling; moreover, with exception of two bromeliad species, there was no single species with a continuous distributional pattern along the mountains from this region, however, the bromeliad distribution varies according to the type of vegetation (Carvajal-Hernández and Krömer 2015, Mondragón-Chaparro *et al.* 2006).

The PCA showed that more than 85 percent of the variation was explained by the principal component 1 and 2 (Fig. 5A), which means that ciliate species composition was influenced by the temperature of the water in the phytotelmata, altitude above sea level and type of vegetation. Almost all bromeliads species were distributed in only one type of vegetation (Fig. 5B), and ciliate species composition was different according to the three clusters that represent the major types of vegetation in the study, i.e. semideciduous tropical forest, montane cloud forest and pine forest (Fig. 5C).

Previous studies of ciliates in tank bromeliads in the Neotropics have documented higher number of species. For example, 61 species were recorded in *Tillandsia heterophylla* where the order Colpodida showed the largest number of species in Mexico (Durán-Ramírez *et al.* 2015). Buosi *et al.* (2014, 2015) observed 92 species and a high diversity of the order Hymenostomatida. They analyzed the effect of the seasonality and location of a population of *Aechmea distichantha* along the margins of River Paraná in Brazil. They suggested that their results were influenced by the proximity of

the bromeliads to the river, where various freshwater ciliate species were able to colonize the plants along the river bank.

Eleven of the 24 species in the present study were only observed in one or two samples, and ciliates were undetectable in 20 percent of samples. Although most of the bromeliads were colonized by ciliates, their presence could be considered as part of the so-called rare biosphere, because they probably cannot establish populations that persist through time but have an unknown ecological significance (Weisse 2014). Patchy distribution was observed in ciliate communities from terrestrial and semiterrestrial environments in South America (Foissner 2016) and contrasts with other ciliate communities in tank bromeliads in the Neotropics. For example, an average of seven ciliate species were observed in bromeliads from central Mexico (Durán-Ramírez *et al.* 2015). In Brazil, Buosi *et al.* (2014, 2015) observed from 13 to 15 species per sample, where *Paracolpoda steinii* and *Cyclidium glaucoma* were the most frequent, and 50 species was the largest number that have been recorded from a single bromeliad, in north Venezuela (Foissner 2016). In the present work the low similarity of species richness between localities, with exception to localities 5 and 6, was consistent with the results from Buosi *et al.* (2015), who found that the species composition in the ciliate communities between geographically proximate bromeliads do not have a considerable similarity. Thus, it suggests that the composition of the ciliate communities from tank bromeliads show variations at spatial and temporal scale in the Neotropics.

As a consequence of differences of microhabitats conditions provided by the plants, by comparing previous results of studies carried out in other regions of the Neotropics, our results exhibit some differences. Foissner (2016) found 50 ciliate species inhabiting four plants from a montane cloud forest, in comparison to the 15 species from 22 bromeliads of locality 2 with the same vegetation. Buosi *et al.* (2014, 2015) reported 92 ciliate species from 72 individuals of *Aechmea distichantha* from rocky walls of the Paraná River, Brazilian Atlantic forest; in the present work, we found 11 species in 10 plants from a fragment of a similar tropical vegetation (locality 7).

The high diversity of tank bromeliads in some regions of the Neotropics makes it possible to collect samples from different genera and species within the same area, and to compare ciliate communities in each plant. In the present study, tank bromeliads of the gen-

era *Pseudalcantarea* and *Tillandsia* were common in humid mountain regions. A remarkable example is *Pseudalcantarea grandis*, a tank bromeliad that possesses one of the largest phytotelmata in the Neotropics, with a high capacity to accumulate more than ten liters of rain water (Benzig 2000). We observed that the ciliate community in *P. grandis* was composed of freshwater ciliate species like *Halteria* spp., terrestrials like *Colpoda maupasi*, and some bromeliad endemic ciliates like *Glaucocides bromelicola*. Moreover, the results (Table 3) reinforce the idea of the absence of host specificity between ciliates and bromeliads, mentioned by Foissner et al. (2003). According to Weisse et al. (2013b), *G. bromelicola* is one of the most common species in this type of microhabitat due to its bactivory and feeding on heterotrophic flagellates of genus *Polytomella*, explaining our observation of this ciliate species in almost half of the samples in this study.

The knowledge of ecology and distribution of other ciliate species endemic to tank bromeliads observed in the present study is still incomplete. An interesting example is *Bromeliothrix metopoides*, widely distributed in the Neotropical region from Mexico to Chile (Weise et al. 2013a). Foissner (2010) and Buosi et al. (2014, 2015) recorded *B. metopoides* in bromeliads from Brazilian forests at altitudes below 300 m ASL. By contrast, Durán-Ramírez et al. (2015) observed this ciliate in bromeliads from a montane cloud forest in Mexico above 1200 m ASL, suggesting that *B. metopoides* inhabits in bromeliads of many types of vegetation at different altitudes along the Neotropics. The endemism of *B. metopoides* to bromeliads has been explained by its unusual narrow ecological niche given by its specific diet, based on bacteria and flagellates, its complex polymorphic life cycle, its ability to encyst, and its type r population strategy (Weisse et al. 2013a, b).

Cotterillia bromelicola (Foissner and Stoeck 2011) is known only from its type locality in Mexico and one site in Costa Rica (Durán-Ramírez et al. 2015, Foissner 2016). In the present study, *C. bromelicola* was observed in *T. gymnobotrya* (from pine forest) and *Tillandsia* sp. (from montane cloud forest), suggesting that, although it can inhabit different bromeliad species, its distribution in this part of the Neotropics is restricted to mountain forests.

We observed the presence of ciliates in *Bromelia pinguin*, a species with a weakly developed phytotelm. This cespitose terrestrial species of morphology type I, is characterized by its almost null capacity to accumu-

late rain water due to its foliar architecture (Benzig 2000). Thus, at least some type I bromeliads as well as those with well-developed phytotelmata (morphology types III and IV), can host ciliate communities. The recovery of *Frontonia pusilla* (Fan et al. 2013), described from a mangrove in Southern China, in *Bromelia pinguin* was unexpected. Its presence may be attributed to the substrate on which this bromeliad grows (i.e. coastal dunes) in this region of the Gulf of Mexico.

Ciliates are preyed by metazoan populations inhabiting bromeliads and other phytotelmata. Wiackowski and Kocerba-Soroka (2017) concluded that the presence/absence of predators (harpacticoid copepods) affects ciliate community structure of the phytotelmata of *Calathea* and *Heliconia*. We observed ants in association with some bromeliad species. These insects might also influence the composition of the protist community through the transport and accumulation of detritus (Carrias et al. 2012).

Regarding the habitat where ciliate species have been previously observed, six species are considered as proper inhabitants of tank bromeliads and six were terrestrial or semiterrestrial (Foissner 1998, 2016; Foissner et al. 2003; Omar and Foissner 2011). Moreover, *Frontonia pusilla* and *L. australiensis* were observed for the first time inhabiting bromeliads in the Neotropics and both are new records for Mexico.

In our study, the number of samples collected at some localities, specially locality 2, could have influenced the high ciliate species richness observed. In addition, Carrias et al. (2012) studying bromeliads in French Guyana, documented that detritus concentration, plant architecture and light incidence were the main factors affecting protist diversity. Fragmentation, sampling effort, effect of area and microclimatic variations may also influence species richness (Rahbek 1995). However, most of the localities in the current study were characterized by various degrees of anthropogenic ecological disturbance including deforestation and agriculture that may produce unknown effects on ciliate community structure in bromeliads. Further studies are needed on the taxonomy, ecology, and distribution of ciliates inhabiting tank bromeliads in the Neotropical region in order to better identify factors, which determine ciliate community structure in these unique habitats.

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Table 3. Presence and ciliate species richness and the bromeliad species where they were recorded.

Ciliate species / Bromeliad species	Ab	Am	Bp	Pg	Pv	Tbc	Tc	Td	Ty	Ti	Tm	Tu	Ts	T1	T2	TS
<i>Anteholosticha</i> sp.									+							1
<i>Bromeliophrya brasiliensis</i>						+		+				+				3
<i>Bromeliothrix metopoides</i>	+						+	+				+				4
<i>Chilodonella uncinata</i>	+	+		+	+	+						+				7
<i>Colpoda cucullus</i>	+		+			+	+	+	+	+			+			8
<i>Colpoda maupasi</i>	+		+	+		+	+					+				6
<i>Cotterillia bromelicola</i>									+			+				2
<i>Drepanomonas revoluta</i>							+					+				2
<i>Euplotopsis</i> sp.					+											1
<i>Frontonia pusilla</i>						+										1
<i>Glaucomides bromelicola</i>	+	+		+	+	+		+	+		+	+	+	+	+	12
<i>Halteria</i> spp.						+	+	+			+	+	+			6
<i>Lambornella</i> spp.	+	+		+	+	+		+	+	+	+	+	+	+		11
<i>Leptopharynx australiensis</i>						+										1
<i>Leptopharynx bromelicola</i>												+	+			2
<i>Leptopharynx bromeliophilus</i>											+	+	+		+	4
<i>Leptopharynx</i> spp.	+						+				+		+			4
<i>Oxytricha</i> sp.					+											1
<i>Paracolpoda steinii</i>						+							+			2
<i>Peritrichia</i> 1										+						1
<i>Peritrichia</i> 2						+										1
<i>Peritrichia telotroch</i>						+										1
<i>Tetrahymena</i> spp.						+			+	+		+	+			5
<i>Vorticella</i> sp.					+											1
Total of species	7	3	10	7	3	10	3	6	6	4	3	6	15	2	2	

For abbreviations of bromeliad species, see table 1. TS = Total bromeliad species where a given ciliate has been recorded.

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Capítulo III

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Checklist of ciliates (Alveolata: Ciliophora) that inhabit in bromeliads from the Neotropical Region

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Abstract

Species from almost all classes of ciliates are prone to be found inhabiting bromeliads in the Neotropics, from Mexico to Brazil, and the Antilles. Studies of ciliates recorded from bromeliads have been carried out from few bromeliad species, mainly in tropical forest. We compiled all available data of free living and sessile ciliates from bromeliads, including their geographic distribution and bromeliad identity. We provide a list of 170 ciliate species that have been recorded in 52 epiphytic and terrestrial bromeliad species, distributed in ten Neotropical countries. Most of the species belong to the Classes Oligohymenophorea, Colpodea and Spirotrichea. The largest number of ciliate species has been recorded in Brazil and Mexico. *Bromeliothrix metopoides* and *Glaucocides bromelicola* were the two species with the widest geographical distribution, 19 species have been recorded only in Mexico, 11 in the Antillean islands, and 89 only in Southamerica. Free living species prevailed over sessile species, and both represent 2% of the total ciliate species number. Sixteen ciliate species have been recorded only inhabiting in bromeliads. Although bromeliads show a high endemicity, their specificity is low in relation to ciliates.

Key words: Bromeliaceae, Endemic ciliates, Neotropics, Phytotelm, Tank bromeliads

Introduction

Ciliates are among the most diverse groups of protists that inhabit in bromeliads. Members of the family Bromeliaceae are an important component of the vascular flora of tropical forests, with more than 3,500 species distributed in the Neotropics (Givnish *et al.* 2007, Gouda & Gouda 2015). Their coalescent leaves allow the accumulation of rainwater and detritus, leading to the formation of a tank or phytotelm (Maguire 1971), which makes possible the establishment of ciliate communities (Foissner *et al.* 2003, Durán-Ramírez *et al.* 2015, Agatha *et al.* 2020).

Most of the taxonomical and ecological studies of ciliates of bromeliads have been carried out in recent years from few bromeliad species with tank morphology, and mainly in tropical forests and agroecosystems (Durán-Ramírez *et al.* 2015; Foissner *et al.* 2003). In a tropical dry-forest of Mexico, Durán-Ramírez & Mayén-Estrada (2018) reported that ciliates can also establish communities in tank-less bromeliads of genera *Bromelia* and *Tillandsia*.

The ciliate community structure in bromeliads can be categorized in two taxonomical components: a) the cosmopolitan species, which have also been recorded from soils, aquatic ecosystems and mosses, and b) species that have been recorded only in the phytotelmata of bromeliads (Foissner *et al.* 2003). According to Dunthorn *et al.* (2012), some genera of ciliates common in freshwater habitats, are absent in bromeliads like *Frontonia*, *Glaucoma*, *Trithigmostoma* and *Paramecium*.

In relation to their habitat preference, ciliates can be found as free living inhabitants along the water column in tank species, between debris accumulated at the bottom of tanks or between the base of the leaves when plants retained little humidity as in the case of tank-less bromeliads, and also as epibionts of metazoa like insects and crustaceans that inhabit in the tanks (Foissner *et al.* 2003). Hyperphoresy among three frogs, ostracods and epibiont ciliates has been recorded in one bromeliad in eastern Brazil (Sabagh *et al.* 2011).

The objective of this work was to provide a checklist of ciliates that inhabit in bromeliads through a compilation of all available records in the literature, including new and unpublished records in Mexican bromeliads and their geographic distribution in the Neotropical Region, and the bromeliads identity if the case. Our results contribute to the knowledge of protist diversity in phytotelmata and distribution of ciliates in the Neotropics.

Methodology

Available records of free living and sessile ciliates species that inhabit in bromeliads from the Neotropical Region were compiled and checked. Also, some new and unpublished Mexican records were included. Their taxonomic status was verified in updated literature, and systematic was according to Lynn (2008). The checklist includes only records of ciliate species, identified with morphological approach (i. e. live observation and silver impregnation techniques), and/or with sequences data. Geographical distribution was included at country level indicating the names of localities when available. If the case, data of bromeliads identity was provided and checked in web resources of TROPICOS® from the Missouri Botanical Garden. References for each record were also provided for all the species.

We included new and unpublished records of ciliate species found in 100 individuals of bromeliads belonging to 13 species, collected during the humid season of years 2015 and 2016 in the Mexican Neotropics. Microphotographs were obtained with a Nikon Labophot-2 microscope equipped with a Nikon Digital Sight DS-L15667 camera, and Photo Microscope Olympus-Provis AX70 and Evolution MP5 megapix camera. Images were rendered by using Helicon Focus 7.6.1.

Bromeliad species referred in the literature were indicated by using the next abbreviations: (Ab) *Aechmea bracteata* (Sw., 1788) Grisebach, 1864, (Ad) *A. distichantha* Lem., 1853, (Af) *A. phanerophlebia* Baker, 1899, (Am) *A. mexicana* Baker, 1879, (Ap) *A. paniculigera* (Sw.) Griseb., 1864, (As) *Aechmea* sp., (Bk) *Bromelia karatas* L. 1753, (Bp) *B. pinguin* L. 1753, (Cb) *Catopsis berteroniana* (Schult. & Schult. f.) Mez, 1896, (Ch) *C. oerstediana* Mez, 1896, (Cs) *C. sessiliflora* (Ruiz & Pavón, 1802) Mez., 1896, (Gm) *Guzmania monostachia* (L.) Rusby ex Mez, 1896, (Gu) *G. musaica* (Linden & André) Mez, 1896, (Gz) *G. scherzeriana* Mez, 1896, (Gs) *Guzmania* sp., (Hi) *Hohenbergia inermis* Mez, 1913, (Hp) *H. penduliflora* (A. Rich.) Mez, 1896, (Hr) *H. proctorii* L. B. Sm., 1960, (Hn) *H. spinulosa* Mez, 1900, (Hu) *H. urbaniana* Mez, 1900, (Hs) *Hohenbergia* sp., (Ni) *Neoregelia ibitipocensis* (Leme) Leme, 1998, (No) *N. oligantha* L. B. Sm., 1955, (Nf) *Nidularium ferdinando-coburgii* Wawra, 1880, (Nm) *N. marigoi* Leme, 1991, (Pg) *Pseudalcantarea grandis* (Schltdl., 1845), (Pv) *P. viridiflora* (Beer, 1856) Pinzón & Barfuss, 2016, (Tc) *Tillandsia concolor* L. B. Sm., 1960 (Td) *T. makoyana* Baker, 1887, (Te) *T. deppeana* Steud., 1841, (Tg) *T. guatemalensis* L. B. Sm., 1949 (Ty) *T. gymnobotrya* Baker, 1887, (Th) *T. heterophylla* E. Morren, 1873, (Ti) *T. imperialis* E. Morren ex Mez., 1935, (Tb) *T. limbata* Schltdl., 1845, (Ta) *T. macrochlamys* Baker, 1888, (Tm) *T. multicaulis* Steudel., 1841, (Tp) *T. polystachia* (L., 1753) L., 1762, (To) *T. prodigiosa* Baker, 1889, (Tr) *T. rothii* Rauh, 1976, (Ts) *Tillandsia* spp., (Vb) *Vriesea bituminosa* Wawra, 1862, (Vf) *V. friburgensis* Mez, 1952, (Vg) *V. gigantea* Gaudich., 1846, (Vh) *V. heterostachys* (Baker) L. B. Sm., 1970, (Vi) *V. incurvata* Gaudich., 1843, (Vp) *V. penduliflora* L. B. Sm., 1943, (Vy) *V. platynema* Gaudich., 1843, (Vs) *V. sanguinolenta* Cogn. & Marchal, 1874, (V1) *Vriesea* sp., (Ws) *Weruahia* sp. and (Wg) *Wittrockia gigantea* (Baker) Leme, 1997.

Ciliate species that occur only in bromeliads were indicated in the checklist with superindex 1, and ciliate species identified by SSU-rDNA sequences were indicated with superindex 2. New and unpublished records of ciliate species from Mexican bromeliads were indicated with the abbreviation ps (present study).

We included a map with the geographical location of localities according to the Neotropical delimitation of Morrone (2017), by using the ArcGis 10.3 software.

Results

We obtained the records of 170 species of ciliates (about 2% of species of phylum Ciliophora), included in two subphyla, 10 classes, 11 subclasses, 30 orders, 64 families, and 112 genera. From these, 16 species have been reported only as inhabitants of bromeliads (endemic). Classes Oligohymenophorea, Colpodea and Spirotrichea included the larger number of species, with 38, 34 and 33 species respectively. Colpodida with 24 species was the order with the largest number of species, and family Oxytrichidae with 15 species. The genus *Colpoda* had the largest species richness (10).

The records of ciliate species belong to ten Neotropical countries (Fig. 1), being Brazil and Mexico those with the largest number of species (79 and 60 respectively). For Mexico, 22 new and unpublished records (Figs. 2-3) were included from six localities, being now the number of ciliate species in bromeliads 6.2% of the total number of ciliates reported in the country (Mayén-Estrada *et al.* 2014). For the rest of the countries included in the present study, 23 species have been recorded in both Dominican Republic and Jamaica, nine in Costa Rica, three species in Chile and Peru, five species in Colombia, 21 species in Ecuador, and 56 species in Venezuela. Ciliate species that establish communities in bromeliads, are not homogeneously distributed along the Neotropical Region. For example, 19 ciliate species have only been recorded in the portion that corresponds to Mexico, 89 only for South American countries, and only 11 in the Antilles (Dominican Republic and Jamaica).

Bromeliads included 52 species (epiphytic and terrestrial), belonging to the genera *Aechmea* Ruiz & Pavón, 1793, *Bromelia* L. 1753, *Catopsis* Grisebach, 1864, *Guzmania* Ruiz & Pavón, 1802, *Hohenbergia* Schult., 1830, *Neoregelia* B. Sm., 1934, *Nidularium* Lem., 1854, *Pseudalcantarea* (Mez) Pinzón & Barfuss, 2016, *Tillandsia* L., 1753, *Vriesea* Lindl., 1843, *Werauhia* J. R. Grant, 1995 and *Wittrockia* Lindm., 1891. According to Givnish *et al.* (2007) and Gouda & Gouda (2015), 3,543 bromeliad species inhabit the Neotropics, from which only 1.4% of the species have been included in studies about ciliate diversity.

Aechmea distichantha in Brazil and *Tillandsia heterophylla* in Mexico, were the two bromeliad species where the largest number of ciliate species has been recorded (Buosi *et al.* 2014 a, b, 2015; Durán-Ramírez *et al.* 2015) (Fig. 4). Although most of the ciliate species were recorded in bromeliads with tank morphology, like those of genera *Aechmea* and *Guzmania*, however, Durán-Ramírez & Mayén-Estrada (2018) recorded some ciliates in tank-less bromeliads of genera *Bromelia* and *Tillandsia* in a dry tropical forest in western Mexico. Other types of forests where ciliates in bromeliads have been identified are tropical forest, montane cloud forest, semideciduous tropical forest, oak and pine forest, farms, coffee plantations, and riparian vegetation (Buosi *et al.* 2014b, 2015; Durán-Ramírez *et al.* 2015; Foissner 2016).

Bromeliothrix metopoides and *Glaucomides bromelicola* were recorded in most countries (nine and seven, respectively), and *G. bromelicola* has been recorded in almost half the number of bromeliad species (27). *Bromeliothrya brasiliensis*, *B. quadrasticha*, *Columnospatha bromelicola*, *Glaucomides bromelicola*, *Gonostomum bromelicola*, *Lambornella trichoglossa*, *Leptopharynx bromelicola*, *L. bromeliophilus*, *Maryna meridiana*, *Orborhabdostyla bromelicola*, *Paroxytricha quadrinucleata*, *Platyophrya bromelicola*, *Pseudovorticella bromelicola*, *Spathidium bromelicola*, *S. bromeliophilum*, and *S. wolfi* occur only in bromeliads. Figure 4 shows the relation between ciliate families recorded from the 52 bromeliad species and the countries where they have been mentioned in the literature. Bromeliads are well known to exhibit a high geographical endemicity which is shown by the colour of the lines, where none of the 52 bromeliad species were present in more than one country. By contrast, ciliate specificity to any bromeliad species is low; however, Bromeliophryidae, Colpodidae and Leptopharyngidae were the most frequent families in bromeliads. On the other hand, the high lineage of *A. distichnatha* and some species of *Tillandsia* reflects that ciliates from only very few bromeliad species have been extensively studied.

Unlike Mexican and West Indies ciliate species, Buosi *et al.* (2014a, b, 2015) and Paz (1980) recorded in South America species from genera *Colpidium*, *Lembadion*, *Litonotus*, *Metopus* and *Paramecium*, previously considered as uncommon inhabitants of bromeliads (Dunthorn *et al.* 2012). Similarly, *Columnospatha bromelicola*, *Enchelariophrya wolfi*, *Protospardium lepidosomatum*, *Spathidium bromelicola*, *S. bromeliophilum* and *S. wolfi* were recorded exclusively in bromeliads from Dominican Republic and Jamaica, but the endemicity of these species to those islands has not been demonstrated.

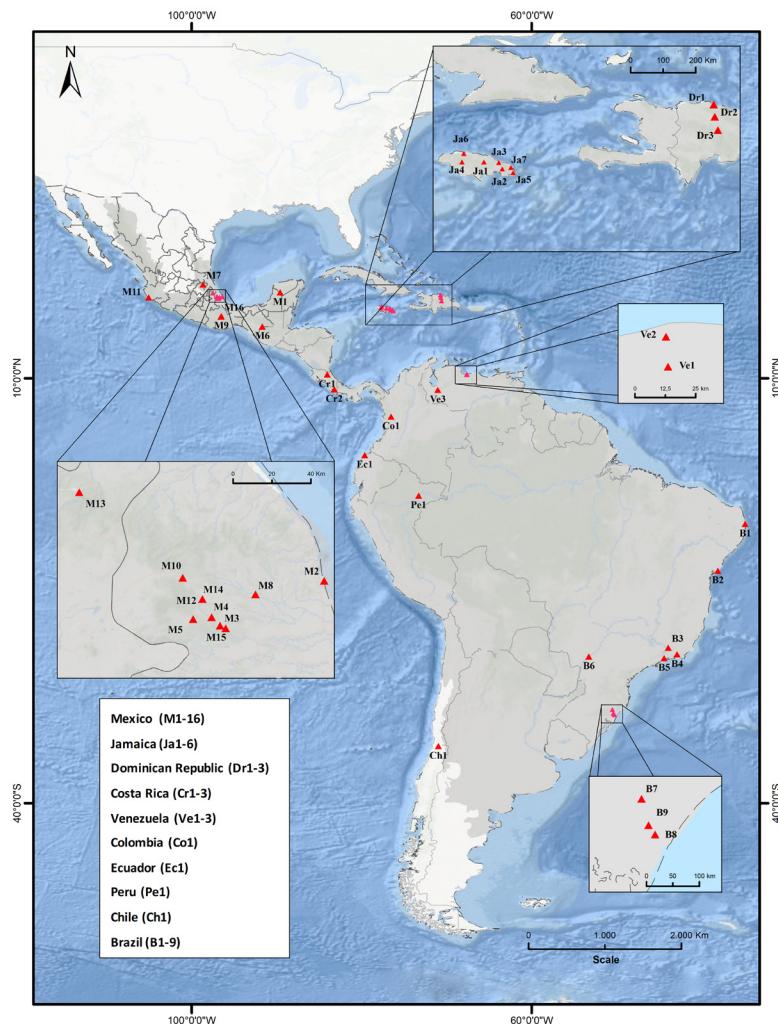


FIGURE 1. Distribution map of the localities in Neotropics referred in the literature where ciliates have been recorded in bromeliads. **Mexico.** **M1**=Biocultural Reserve Kaxil Kiuic, near Oxkutzcab, **M2**=Coastal Research Center La Mancha/CICOLMA, **M3**=Coffee plantation Arcos Vegas y Rincón de Yeguas, Tuzamapan, **M4**=Coffe plantation Virginia Armand, near Coatepec, **M5**=Coffee plantation La Onza, near Coatepec, **M6**=Dos Lagunas, near Village of Tzsicao, **M7**=El Tegolome, near the town of Tlanchinol, **M8**=Environmental Management Area Nace el Río, Descabezadero, **M9**=Ixtlán de Juárez, Oaxaca, **M10**=La Joya, Acajete, **M11**=Reserve of the Biosphere Chamela-Cuixmala, **M12**=Santuario del Bosque de Niebla, near Xalapa, **M13**=Surroundings of Reserva Azul, near the town of Cuetzalan, **M14**=Surroundings of the town of Xalapa, **M15**=Tlacuitlapa, Jalcomulco, **M16**=Village El Cerezal, near Santa Catarina Ixtepeji. **Jamaica.** **Ja1**=Mount Diablo, northwest of Spanish Town, **Ja2**=Near the Village of Ecclesdown, **Ja3**=Northern slope of the Blue Mountains, surroundings of the village of Silver Hill, **Ja4**=Parish Saint Elizabeth, near the road between the villages of Aberdeen and Quick Step, **Ja5**=Saint Thomas, at the Eastern tip of Jamaica, near the villages of Golden Grove and Rowlandsfield, **Ja6**=Surroundings of the village of Quick Step in Cockpit Country, **Ja7**=Upper Cedar Valley, southern slope of the Blue Mountains. **Dominican Republic.** **Dr1**=Botanical Garden on the Pico Isabel de Torres, 800 m high mountain on the outskirts of the town of Puerto Plata, **Dr2**=North slope of the Cordillera Central, in the surroundings of the waterfall Salto de Jimenoa, **Dr3**=Santiago de los Caballeros. **Venezuela.** **Ve1**=South margin of the Henri Pittier National Park, Biological Station Rancho Grande, **Ve2**=North border of the Henri Pittier National Park, surroundings of the village of Choroni, **Ve3**=Sierra Nevada National Park. **Costa Rica.** **Cr1**=bank of the Río Sarapiquí, Selva Verde National Park, **Cr2**=Tropic Station La Gamba. **Colombia.** **Co1**=Lloró. **Ecuador.** **Ec1**=Esmeraldas, underneath Alto Tambo. **Peru.** **Pe1**=Peru. **Chile.** **Ch1**=Chile. **Brazil.** **B1**=Nature Reserve Mata do Buraquinho in the town of João Pessoa, Paraíba, **B2**=Surroundings of the Village of Praia do Forte, about 81 km North of the town of Salvador, Bahia, **B3**=Parque Estadual do Ibitipoca, Minas Gerais, **B4**=Rio de Janeiro, **B5**=Bracuhy Port, Angra dos Reis, **B6**=Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná, **B7**=Garapia River, Rio Grande do Sul, **B8**=Maquiné River basin, Rio Grande do Sul, **B9**=Pró-Mata de São Francisco de Paula, Rio Grande do Sul.

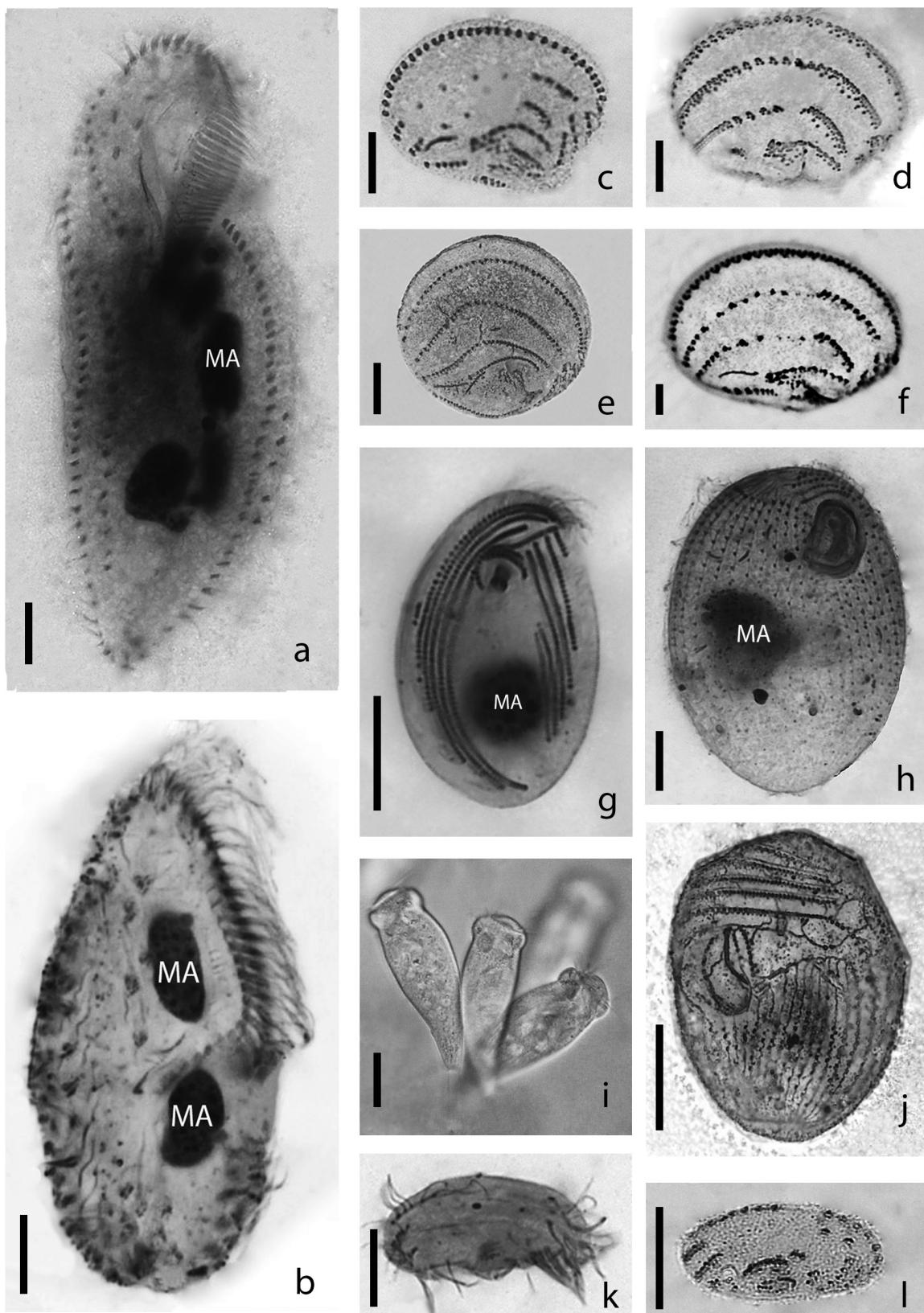


FIGURE 2. Ciliate species from Mexican bromeliads included in the present study: a. *Fragmocirrus espeletiae*, b. *Gonostomum bromelicola*, c. *Leptopharynx bromeliophilus*, d. *L. brasiliensis*, e. *L. bromelicola*, f. *L. costatus*, g. *Chilodonella uncinata*, h. *Glaucomides bromelicola*, i. *Epistylis plicatilis* (in vivo), j. *Bromeliophrya brasiliensis*, k. *Drepanomonas revoluta*, l. *D. sphagni*. MA-macronucleus; a, b, g, h, k: cells with protargol procedure (Foissner 2014); c-f, j, l. Cells impregnated with the dry silver nitrate method (Foissner 2014). Scale bars: 10µm.

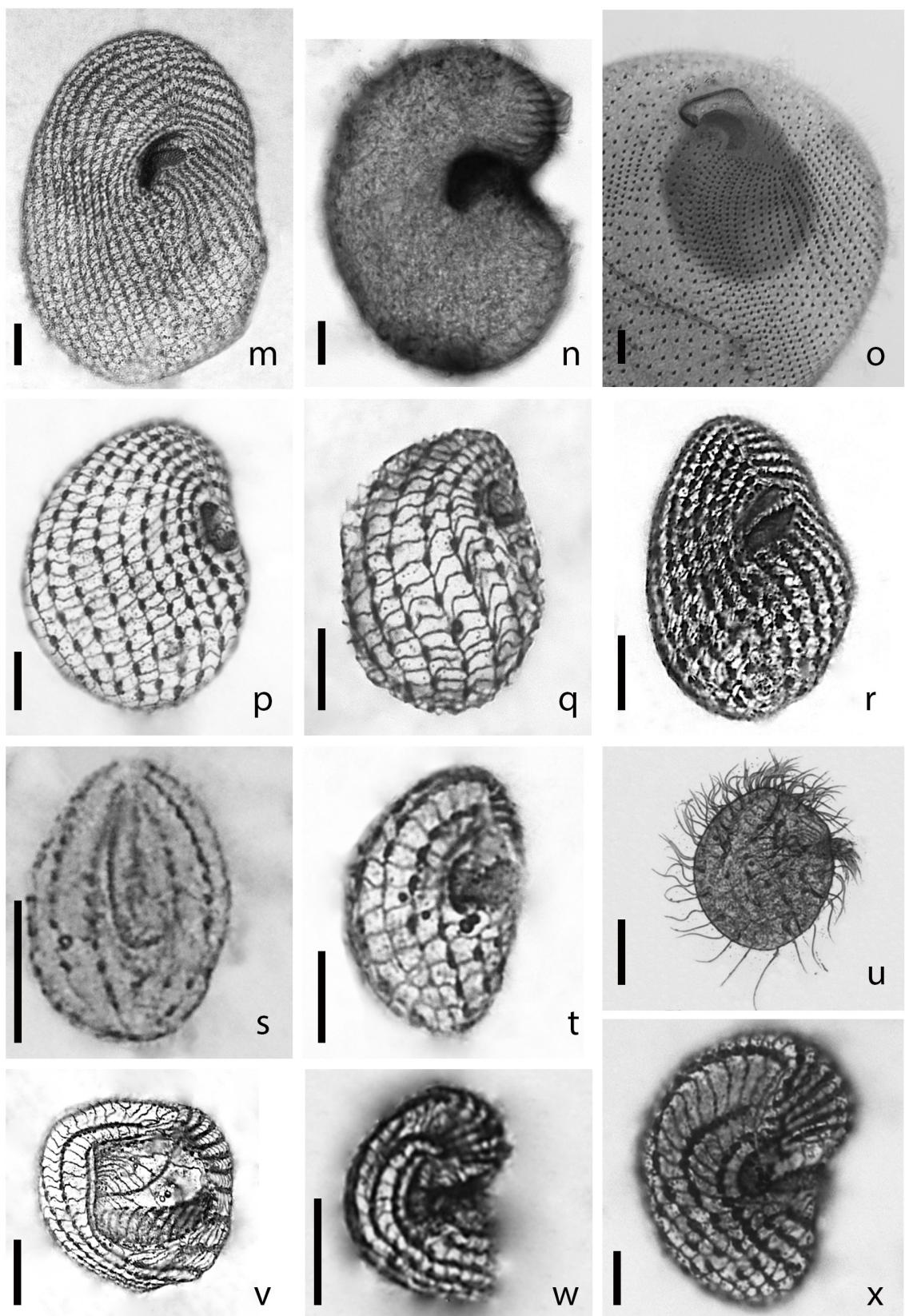
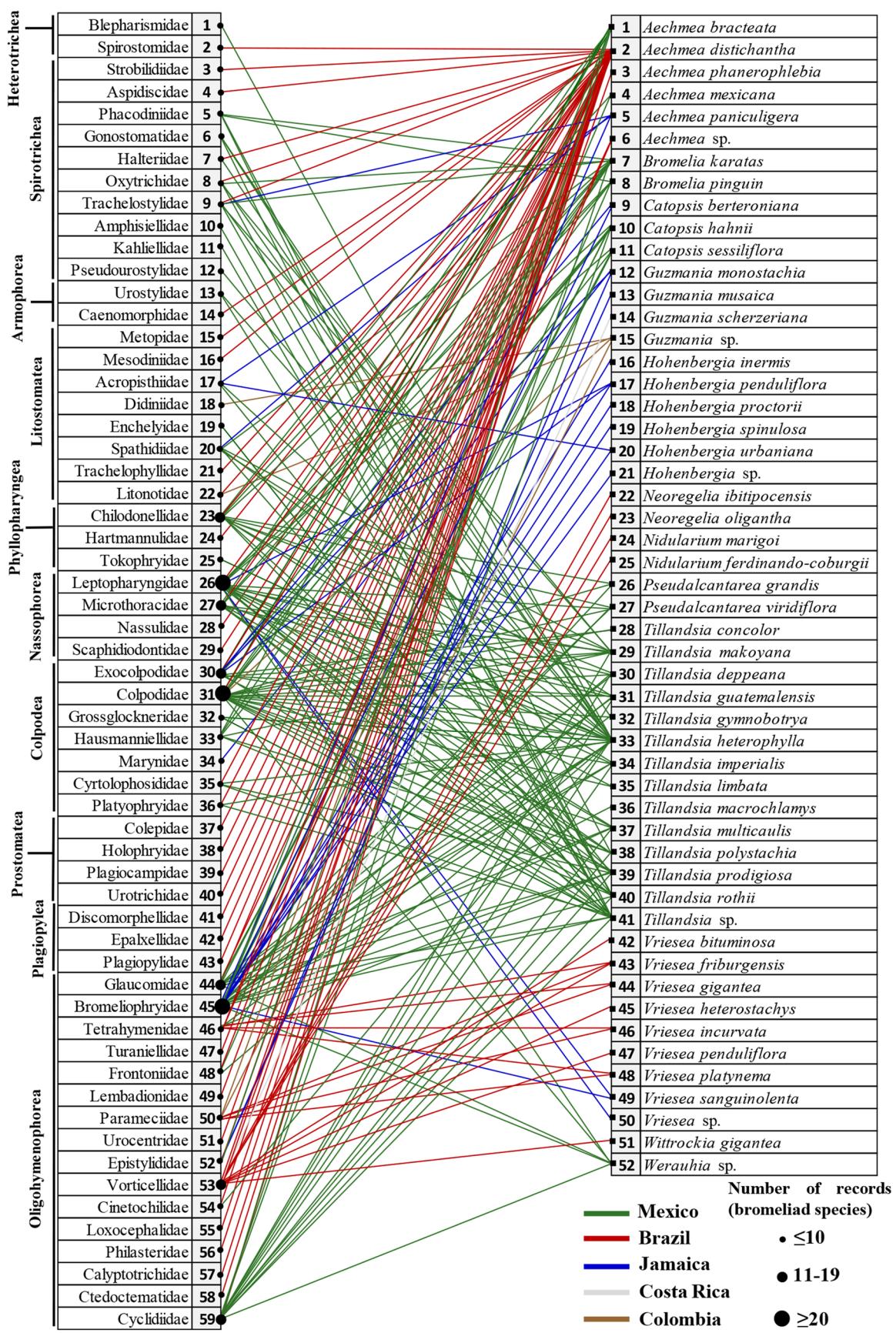


FIGURE 3. Ciliate species from Mexican bromeliads included in the present study: m. *Colpoda lucida*, n. *C. cucullus*, o. *C. cavicola*, p. *C. maupasi*, q. *Emarginatophrya aspera*, r. *C. inflata*, s. *Cyclidium glaucoma*, t. *Paracolpoda lajacola*, u. *P. steinii*, v. *Bromeliothrix metopoides* macrostome, w. microstomous theront of *B. metopoides*, x. microstomous trophont of *B. metopoides*. MA-macronucleus; m, p-x: Cells impregnated with the dry silver nitrate method (Foissner, 2014); n. Cell impregnated with nigrosine; o: Cells with silver carbonate impregnation (Fernández-Galiano 1976). Scale bars: 10µm.



†The size of the circles in the left column indicates the number of bromeliad species where ciliate families have been recorded.

FIGURE 4. Network of ciliate-bromeliad interaction. Ciliate species are represented grouped in families according to the countries where they were recorded.

Checklist

Phylum Ciliophora Doflein, 1901

Subphylum Postciliodesmatophora Gerassimova & Seravin, 1976

Class Heterotrichea Stein, 1859

Order Heterotrichida Stein, 1859

Family Blepharismidae Jankowski in Small & Lynn, 1985

Genus *Blepharisma* Perty, 1849

***Blepharisma hyalinum* Perty, 1849**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

***Blepharisma steini* Kahl, 1932**

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Family Spirostomidae Stein, 1867

Genus *Spirostomum* Ehrenberg, 1834

***Spirostomum ambiguum*² (Müller, 1786) Ehrenberg, 1835**

Distribution. JAMAICA: (Dunthorn *et al.* 2012).

***Spirostomum minus* Roux, 1901**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subphylum Intramacronucleata Lynn, 1996

Class Spirotrichea Bütschli, 1889

Subclass Choreotrichia Small & Lynn, 1985

Order Choreotrichida Small & Lynn, 1985

Family Strobilidiidae Kahl in Doflein & Reichenow, 1929

Genus *Rimostrombidium* Jankowski, 1978

***Rimostrombidium humile* (Penard, 1922) Petz & Foissner, 1992**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subclass Hypotrichia Stein, 1859

Order Euplotida Small & Lynn, 1985

Suborder Euplotina Small & Lynn, 1985

Family Aspidiscidae Ehrenberg, 1830

Genus *Aspidisca* Ehrenberg, 1830

Aspidisca cicada (Müller, 1786) Claparède & Lachmann, 1858

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Aspidisca lynceus (Müller, 1773) Ehrenberg, 1830

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subclass Phacodiniidia Small & Lynn, 1985

Order Phacodiniida Small & Lynn, 1985

Family Phacodiniidae Corliss, 1979

Genus *Phacodinium* Prowazek, 1900

Phacodinium metchnikoffi (Certhes, 1891) Prowazek, 1900

Distribution. MEXICO: Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Bp, Tp, Tr).

Subclass Stichotrichia Small & Lynn, 1985

Order Sporadotrichida Fauré-Fremiet, 1961

Family Gonostomatidae Small & Lynn, 1985

Genus *Cotterillia* Foissner & Stoeck, 2011

*Cotterillia bromelicola*² Foissner & Stoeck, 2011

Distribution. COSTA RICA: (Dunthorn *et al.* 2012; Foissner 2016). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); La Joya (Durán-Ramírez *et al.* 2019), (Ty); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Ts); Surroundings of the town of Xalapa (Foissner & Stoeck 2011), (Th).

Family Halteriidae Claparède & Lachmann, 1858

Genus *Halteria* Dujardin, 1841

Halteria grandinella (Müller, 1773) Dujardin, 1841

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Meseres* Schewiakoff, 1893

Meseres corlissi Petz & Foissner, 1992

Distribution. DOMINICAN REPUBLIC: (Foissner *et al.* 2003).

Family Oxytrichidae Ehrenberg, 1830

Genus *Cyrtohymena* Foissner, 1989

Cyrtohymena quadrinucleata (Dragesco & Njiné, 1971) Foissner, 1989

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Oxytricha* Bory de St. Vincent, 1824, in Lamouroux, Bory de St. Vincent & Deslongchamps, 1824

Oxytricha granulifera Foissner & Adam, 1983

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Oxytricha longigranulosa² Berger & Foissner, 1989

Distribution. ECUADOR: (Foissner *et al.* 2003). JAMAICA: (Dunthorn *et al.* 2012).

Oxytricha opisthomuscorum Foissner, Blatterer, Berger & Kohmann, 1991

Distribution. MEXICO: Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Oxytricha ottowi² Foissner, 1996

Distribution. BRAZIL: (Dunthorn *et al.* 2012). JAMAICA: (Dunthorn *et al.* 2012).

Oxytricha setigera Stokes, 1891

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Genus *Paroxytricha* Foissner 2016

Paroxytricha quadrinucleata[†] Foissner, 2016

Distribution. BRAZIL: (Foissner 2016). CHILE: (Foissner 2016). JAMAICA: (Foissner 2016). MEXICO: surroundings of the town of Xalapa (Foissner 2016), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Pattersoniella* Foissner, 1987

Pattersoniella vitiphila Foissner, 1987

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tr).

Genus *Rigidocortex* Berger, 1999

Rigidocortex octonucleatus (Foissner, 1988) Berger, 1999

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Rubrioxytricha* Berger, 1999

Rubrioxytricha haematoplasma (Blatterer & Foissner, 1990) Berger, 1999

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná [recorded as *Oxytricha haematoplasma*], (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Sterkiella* Foissner, Blatterer, Berger & Kohmann, 1991

Sterkiella cavigola (Kahl, 1935) Foissner, Blatterer, Berger & Kohmann, 1991

Distribution. MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Sterkiella histriomuscorum Foissner, Blatterer, Berger & Kohmann, 1991

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Stylonychia* Ehrenberg, 1830

Stylonychia mytilus (Müller, 1773) Ehrenberg, 1830

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Urosomoida* Hemberger in Foissner, 1982

Urosomoida agiliformis Foissner, 1982

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Urosomoida reticulata Foissner, Agatha & Berger, 2002

Distribution. COSTA RICA: (Foissner, 2003a); Rio Sarapiquí, Selva Verde National Park (Foissner *et al.* 2002).

Family Trachelostylidae Small & Lynn, 1985

Genus *Gonostomum* Sterki, 1878

Gonostomum affine (Stein, 1859) Sterki, 1878

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th, Ts). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Gonostomum bromelicola¹ Foissner 2016

Distribution. JAMAICA: (Foissner 2016), (Ap). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tr).

Gonostomum kuehnelti Foissner, 1987

Distribution. MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Genus *Hemisincirra* Hemberger, 1985

Hemisincirra inquieta Hemberger, 1985

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Order Stichotrichida Fauré-Fremiet, 1961

Family Amphisellidae Jankowski, 1979

Genus *Lamtostyla* Buitkamp, 1977

Lamtostyla australis (Blatterer & Foissner, 1988) Petz & Foissner, 1996

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Incertae sedis in family Amphisellidae

Genus *Circinella* Foissner, 1994

Circinella filiformis (Foissner, 1982) Foissner, 1994

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Family Kahliellidae Truffau, 1979

Incertae sedis in family Kahliellidae

Genus *Fragmocirrus* Foissner, 2000

Fragmocirrus espeletiae Foissner, 2000

Distribution. MEXICO: El Tegolome, near the town of Tlanchinol (ps), (Ts). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Order Urostylida Jankowski, 1979

Family Pseudourostylidae Jankowski, 1979

Genus *Pseudourostyla* Borror, 1972

Pseudourostyla franzii Foissner, 1987

Distribution. MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Family Urostylidae Bütschli, 1889

Genus *Anteholosticha* Berger, 2003

Anteholosticha antecirrata Berger, 2006

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa [recorded as *Holosticha muscorum*] (Durán-Ramírez *et al.* 2015), (Th).

Genus *Caudiholosticha* Berger, 2003

Caudiholosticha tetracirrata (Buitkamp & Wilbert, 1974) Berger, 2003

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Genus *Uroleptus* Ehrenberg, 1831

Uroleptus lepisma (Wenzel, 1953) Foissner, 1998

Distribution. DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Class Armophorea Lynn, 2004

Order Armophorida Jankowksi, 1964

Family Caenomorphidae Poche, 1913

Genus *Caenomorpha* Perty, 1852

Caenomorpha medusala Perty, 1852

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Metopidae Kahl, 1927

Genus *Brachonella* Jankowski, 1964

Brachonella spiralis McMurrich, 1884

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Metopus* Claparède & Lachmann, 1858

Metopus minor Kahl, 1927

Distribution. ECUADOR: (Foissner *et al.* 2003)

Metopus palaformis Kahl, 1927

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Metopus setosus Kahl, 1927

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Metopus striatus McMurrich, 1884

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Class Litostomatea Small & Lynn, 1981

Subclass Haptoria Corliss, 1974

Order Cyclotrichiida Jankowski, 1980

Family Mesodiniidae Jankowski, 1980

Genus *Mesodinium* Stein, 1863

Mesodinium pulex (Claparède & Lachmann, 1859) Stein, 1867

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Order Haptorida Corliss, 1974

Family Acropisthiidae Foissner & Foissner, 1988

Genus *Coriplites* Foissner, 1988

Coriplites proctori Oertel, Wolf, Al-Rasheid & Foissner, 2009

Distribution. JAMAICA: Dunthorn *et al.* 2012 (Ap, Hu); Parish Saint Elizabeth, near the road between the villages of Aberdeen and Quick Step (Oertel *et al.* 2009), (Ap). MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Ixtlán de Juárez (Durán-Ramírez *et al.* 2015), (To); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Genus *Fuscheria* Foissner, 1983

Fuscheria terricola² Berger, Foissner & Adam, 1983

Distribution. BRAZIL: Rio de Janeiro (Dunthorn *et al.* 2012).

Family Didiniidae Poche, 1913

Genus *Didinium* Stein, 1859

Didinium nasutum (Müller, 1773) Stein, 1859

Distribution. COLOMBIA: Lloró (Paz 1980), (Gs).

Family Enchelyidae Ehrenberg, 1838

Genus *Enchelys* Müller, 1773

Enchelys tumida Foissner 2016

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Family Pseudoholophryidae Berger, Foissner & Adam, 1984

Genus *Pseudoholophrya* Berger, Foissner & Adam, 1984

Pseudoholophrya terricola Berger, Foissner & Adam, 1984

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Family Spathidiidae Kahl in Doflein & Reichenow, 1929

Genus *Arcuospathidium* Foissner, 1984

Arcuospathidium cultriforme scalpriforme (Kahl, 1930) Foissner, 2003

Distribution. MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Arcuospathidium muscorum muscorum (Dragesco & Dragesco-Kernéis, 1979) Foissner, 1984

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Arcuospathidium namibiense tristicha Foissner, Agatha & Berger, 2002

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Bryophyllum* Kahl, 1931

Bryophyllum paucistriatum Foissner, Agatha & Berger, 2002

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Columnospatha* Foissner, 2016

Columnospatha bromelicola¹(Foissner *et al.* 2014) Foissner, 2016

Distribution. JAMAICA: Upper Cedar Valley, southern slope of the Blue Mountains [recorded as *Arcuopathidium bromelicola*] (Foissner 2016; Foissner *et al.* 2014).

Genus *Enchelariophrya* Foissner, 2016

Enchelariophrya wolfi Foissner, 2016

Distribution. JAMAICA: Surroundings of the village of Quick Step in Cockpit Country (Foissner 2016), (Ap).

Genus *Epispadhidium* Foissner, 1984

Epispadhidium ascendens (Wenzel, 1955) Foissner, 1987

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Epispadhidium terricola Foissner, 1987

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Protospathidium* Dragesco & Dragesco-Kernéis in Foissner, 1984

Protospathidium lepidosomatum Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

Distribution. JAMAICA: Upper Cedar Valley, southern slope of the Blue Mountains (Foissner *et al.* 2014).

Genus *Spathidium* Dujardin, 1841

Spathidium bromelicola¹ Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

Distribution. DOMINICAN REPUBLIC: Botanical Garden on the Pico Isabel de Torres, 800 m high mountain on the outskirts of the town of Puerto Plata (Foissner *et al.* 2014).

Spathidium bromeliophilum¹ Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

Distribution. JAMAICA: Upper Cedar Valley, southern slope of the Blue Mountains (Foissner *et al.* 2014).

Spathidium claviforme Kahl, 1930

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Spathidium procerum Kahl, 1930

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Spathidium spathula (Müller, 1773) Moody, 1912

Distribution. COLOMBIA: Lloró (Paz 1980), (Gs). MEXICO: Dos Lagunas, near village of Tzsíscalo (ps); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tr).

Spathidium wolfi¹ Foissner, Wolf, Kumar, Xu & Quintela-Alonso, 2014

Distribution. JAMAICA: Mount Diablo, northwest of Spanish Town (Foissner *et al.* 2014).

Family Trachelophyllidae Kent, 1882

Genus *Enchelyodon* Claparède & Lachmann, 1859

Enchelyodon gondwanensis Foissner, 2016

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Lagynophrya* Kahl, 1927

Lagynophrya acuminata Kahl, 1953

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b), (Ad).

Order Pleurostomatida Schewiakoff, 1896

Family Litonotidae Kent, 1882

Genus *Acineria* Dujardin, 1841

Acineria uncinata Tucolesco, 1962

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Litonotus* Wrześniowski, 1870

Litonotus crystallinus (Vuxanovici, 1960) Foissner, Berger, Blatterer & Kohmann, 1995

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Litonotus fasciola Ehrenberg, 1870

Distribution. COLOMBIA: Lloró (Paz 1980), (Gs).

Litonotus varsaviensis (Wrześniowski, 1866) Wrześniowski, 1870

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Class Phyllopharyngea de Puytorac *et al.* 1974

Subclass Cyrtophoria Fauré-Frémiel in Corliss, 1956

Order Chlamydodontida Deroux, 1976

Family Chilodonellidae Deroux, 1970

Genus *Chilodonella* Strand, 1928

Chilodonella uncinata (Ehrenberg, 1838) Strand, 1928

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). ECUADOR: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coffee plantation Arcos Vegas y Rincón de Yeguas, Tuzamapan (Durán-Ramírez *et al.* 2019), (Ab, Am); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015),

(Th); (Durán-Ramírez *et al.* 2019), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); El Tegolome, near the town of Tlanchinol (ps), (Ti); Environmental Management Area Nace el Río, Descabezadero (Durán-Ramírez *et al.* 2019), (Ab, Pg); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Pv, Te, Ts); (ps), (Te); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To).

Genus *Pseudochilodonopsis* Foissner, 1979

Pseudochilodonopsis algivora (Kahl, 1931) Foissner, 1979

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Incertae sedis in family Chilodonellidae

Genus *Odontochlamys* Certes, 1891

Odontochlamys gouraudi Certes, 1891

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th). Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Ab, Bk, Td).

Order Dysteriida Deroux, 1976

Family Hartmannulidae Poche, 1913

Genus *Trochilioides* Kahl, 1931

Trochilioides recta (Kahl, 1928) Kahl, 1931

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subclass Suctoria Claparède & Lachmann, 1858

Order Endogenida Collin, 1912

Family Tokophryidae Jankowski in Small & Lynn, 1985

Genus *Tokophrya* Bütschli, 1889

Tokophrya infusionum² (Stein, 1859) Buetschli, 1889

Distribution. MEXICO: (Dunthorn *et al.* 2012); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Class Nassophorea Small & Lynn, 1981

Order Microthoracida Jankowski, 1967

Family Leptopharyngidae Kahl, 1926

Genus *Leptopharynx* Mermod, 1914

***Leptopharynx australiensis* Omar & Foissner, 2011**

Distribution. MEXICO: Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019), (Bp).

***Leptopharynx brasiliensis* Foissner & Omar, 2012**

Distribution. MEXICO: Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Tp, Tr); Dos Lagunas, near village of Tzsiscão (ps), (Tg).

***Leptopharynx bromelicola*^{1,2} Foissner, Wolf, Yashchenko & Stoeck, 2011**

Distribution. COSTA RICA: (Foissner *et al.* 2011). DOMINICAN REPUBLIC: (Foissner *et al.* 2011). ECUADOR: (Foissner *et al.* 2011). JAMAICA: (Dunthorn *et al.* 2012), (Hp); Northern slope of the Blue Mountains, surroundings of the village of Silver Hill (Foissner *et al.* 2011). MEXICO: (Foissner *et al.* 2011); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); El Tegolome, near the town of Tlanchinol (ps), (Ti); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Tm, Ts); (ps), (Cs, Te, Tm, Ts); Village El Cerezal, near Santa Catarina Ixtapejí (ps), (To). PERU: (Foissner *et al.* 2011).

***Leptopharynx bromeliophilus*¹ Omar & Foissner, 2011**

Distribution. JAMAICA: (Dunthorn *et al.* 2012), (Vs); near the village of Ecclesdown (Omar & Foissner 2011), (V1). MEXICO: Omar & Foissner 2011, (Th); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Tb); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near village of Tzsiscão (ps), (Ch, Tg, Ws); El Tegolome, near the town of Tlanchinol (ps), (Ti); Ixtlán de Juárez, Oaxaca (Durán-Ramírez *et al.* 2015), (To); La Joya, Acajete (Durán-Ramírez *et al.* 2019), (Ts); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Bp, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Tm, Ts); Surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs, Th); Village El Cerezal, near Santa Catarina Ixtapejí (ps), (To).

***Leptopharynx costatus* Mermod, 1914**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad); (Foissner *et al.* 2003). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: (Foissner *et al.* 2011), (Th); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near village of Tzsiscão (ps), (Tg); El Tegolome, near the town of Tlanchinol (ps), (Ti); Ixtlán de Juárez, Oaxaca (Durán-Ramírez *et al.* 2015), (To); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (ps), (Cs, Pv, Te, Tm); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs, Th); Village El Cerezal, near Santa Catarina Ixtapejí (ps), (To); VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Genus *Pseudomicrothorax* Mermod, 1914

***Pseudomicrothorax agilis* Mermod, 1914**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Microthoracidae Wrześniowski, 1870

Genus *Drepanomonas* Fresenius, 1858

Drepanomonas exigua bidentata Foissner, 1999

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Drepanomonas minuta Foissner & Omar, 2014

Distribution. MEXICO: Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tp).

Drepanomonas pauciciliata Foissner, 1987

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Drepanomonas revoluta Penard, 1922

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscao (ps), (Tg, Tm); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Bp, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Ts); Surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th).

Drepanomonas sphagni Kahl, 1931

Distribution. MEXICO: Surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th).

Genus *Microthorax* Engelmann, 1862

Microthorax pusillus Engelmann, 1862

Distribution. ECUADOR: (Foissner *et al.* 2003). BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Stammeridium* Wenzel, 1969

Stammeridium kahli (Wenzel, 1953) Wenzel, 1969

Distribution. BRAZIL: (Foissner *et al.* 2003).

Order Nassulida Jankowski, 1967

Family Nassulidae de Fromentel, 1874

Genus *Nassulides* Foissner, Agatha & Berger, 2002

Nassulides pictus (Greeff, 1888) Foissner, Agatha & Berger, 2002

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná [recorded as *Nassula picta*] (Buosi *et al.* 2014b, 2015), (Ad).

Order Synhymeniida de Puytorac *et al.* 1978

Family Scaphidiodontidae Deroux in Corliss, 1979

Genus *Chilodontopsis* Blochmann, 1895

***Chilodontopsis depressa* (Perty, 1852) Blochmann, 1895**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Class Colpodea Small & Lynn, 1981

Order Bryometopida Foissner, 1985

Family Bryometopidae Jankowski, 1980

Genus *Bryometopus* Kahl, 1932

***Bryometopus triquetus* Foissner, 1993**

Distribution. BRAZIL: (Foissner *et al.* 2003).

Family Kreyellidae Foissner, 1979

Genus *Microdiaphanosoma* Wenzel, 1953

***Microdiaphanosoma arcuatum* (Grandori & Grandori, 1934) Wenzel, 1953**

Distribution. ECUADOR: (Foissner *et al.* 2003).

Order Bryophryida de Puytorac, Perez-Paniagua & Perez-Silva, 1979

Family Bryophryidae de Puytorac, Perez-Paniagua & Perez-Silva, 1979

Genus *Notoxoma* Foissner, 1993

***Notoxoma parabryophryides* Foissner, 1993**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Order Colpodida de Puytorac *et al.* 1974

Family Colpodidae Bory de St. Vincent, 1826

Genus *Bresslaua* Kahl, 1931

***Bresslaua insidiatrix* Claff, Dewey & Kidder, 1941**

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Bresslaua vorax Kahl, 1931

Distribution. COLOMBIA: (Paz 1980), (Gs). BRAZIL: (Foissner *et al.* 2003).

Genus *Colpoda* Müller, 1773

Colpoda cavicola Kahl, 1935

Distribution. MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab).

Colpoda cucullus (Müller, 1773) Gmelin, 1790

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). ECUADOR: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019), (Bp, Tc); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Tb, Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscão (ps), (Cs, Ch, Tg, Tm, Ts); El Tegolome, near the town of Tlanchinol (ps), (Ti, Ts); Environmental Management Area Nace el Río, Descabezadero (Durán-Ramírez *et al.* 2019), (Ab); La Joya, Acajete (Durán-Ramírez *et al.* 2019), (Ty); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Te, Ts); (ps), (Cs, Pv, Te); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs, Th); Village El Cerezal, near Santa Catarina Ixtépeji (ps), (To). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Colpoda edaphoni Foissner, 1980

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Colpoda ellioti Bradbury & Outka, 1967

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Colpoda henneguyi Fabré-Domergue, 1889

Distribution. MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Ixtlán de Juárez (Durán-Ramírez *et al.* 2015), (To); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Colpoda inflata (Stokes, 1884) Kahl, 1931

Distribution. BRAZIL: (Foissner *et al.* 2003); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); Village El Cerezal, near Santa Catarina Ixtépeji (ps), (To). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts); Sierra Nevada National Park (Foissner 2016).

Colpoda lucida Greeff, 1888

Distribution. BRAZIL: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscão (ps), (Tg);

Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To).

***Colpoda magna* (Gruber, 1879) Lynn, 1978**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

***Colpoda maupasi* Enriques, 1908**

Distribution. DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019), (Bp, Tc); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscaco (ps), (Tg, Tm, Ws); El Tegolome, near the town of Tlanchinol (ps), (Ti, Tm, Ts); Environmental Management Area Nace el Río, Descabezadero (Durán-Ramírez *et al.* 2019), (Ab, Pg); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Ab, Bk, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Ts); (ps), (Cs, Te); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs, Th); Tlacuitlapa, Jalcomulco (Durán-Ramírez *et al.* 2019), (Ab, Pg); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

***Colpoda praestans* Penard, 1922**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Incertae sedis in Family Colpodidae

Genus *Paracolpoda* Lynn, 1987

***Paracolpoda lajacola* Foissner 2016**

Distribution. MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Dos Lagunas, near Village of Tzsiscaco (ps), (Tg); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To).

***Paracolpoda steinii* (Maupas, 1883) Lynn, 1974**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná [recorded as *Colpoda steinii*] (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: [recorded as *Colpoda steinii*] (Foissner *et al.* 2003). ECUADOR: [recorded as *Colpoda steinii*] (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019), (Bp); Dos Lagunas, near Village of Tzsiscaco (ps), (Ch, Tg, Ws); Coffee plantation La Onza, near Coatepec [recorded as *Colpoda steinii*] (Durán-Ramírez *et al.* 2015), (Th); El Tegolome, near the town of Tlanchinol (ps), (Ti, Tm, Ts); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Ab, Bk, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa [recorded as *Colpoda steinii*] (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Ts); (ps), (Tm); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Family Exocolpodidae Foissner, Agatha & Berger, 2002

Genus *Bromeliothrix* Foissner, 2010

***Bromeliothrix metopoides*² Foissner, 2010**

Distribution. BRAZIL: (Dunthorn *et al.* 2012; Weisse *et al.* 2013a, b); Nature Reserve Mata do Buraquinho in the town of João Pessoa, Paraíba (Foissner 2010); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). CHILE: (Foissner 2010). COSTA RICA: (Foissner 2010). DOMINICAN REPUBLIC: (Foissner 2010). ECUADOR: (Foissner 2010). JAMAICA: (Dunthorn *et al.* 2012), (Cb, Gm, Hp); (Foissner 2010). MEXICO: (Foissner 2010); Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019) (Tc); Coffee plantation Arcos Vegas y Rincón de Yeguas, Tuzamapan (Durán-Ramírez *et al.* 2019) (Ab); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Th); Dos Lagunas, near Village of Tzsiscão (ps), (Ch, Tg); Environmental Management Area Nace el Río, Descabezadero (Durán-Ramírez *et al.* 2019) (Ab); Ixtlán de Juárez (Durán-Ramírez *et al.* 2015), (To); Reserve of the Biosphere Chamele-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Ts); (ps), (Te, Ts); Surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To). PERU: (Foissner 2010). VENEZUELA: (Foissner 2010).

Family Grossglockneridae Foissner, 1980

Genus *Grossglockneria* Foissner, 1980

***Grossglockneria hyalina* Foissner, 1985**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016)

Genus *Mykophagophrys* Foissner, 1995

***Mykophagophrys terricola* (Foissner, 1985) Foissner, 1995**

Distribution. MEXICO: Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Genus *Nivaliella* Foissner, 1980

***Nivaliella plana* Foissner, 1980**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Genus *Pseudoplatyophrya* Foissner, 1980

***Pseudoplatyophrya nana* (Kahl, 1926) Foissner, 1980**

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

***Pseudoplatyophrya saltans* Foissner, 1988**

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Family Hausmanniellidae Foissner, 1987

Genus *Bresslauides* Blatterer & Foissner, 1988

Bresslauides terricola (Foissner, 1987) Foissner, 1993

Distribution. MEXICO: Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tr).

Genus *Emarginatophrya* Foissner 2016

Emarginatophrya aspera (Kahl, 1926) Foissner 2016

Distribution. MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Dos Lagunas, near Village of Tzsiscaco (ps), (Tg); Reserve of the Biosphere Chamela-Cuixmala [recorded as *Colpoda aspera*] (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tp, Tr); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs).

Genus *Hausmanniella* Foissner, 1984

Hausmanniella patella (Kahl, 1931) Foissner, 1984

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Family Marynidae Poche, 1913

Genus *Maryna* Gruber, 1879

Maryna meridiana¹ Foissner 2016

Distribution. COSTA RICA: (Foissner 2016). JAMAICA: (Foissner 2016), (Gm).

Order Cyrtolophosidida Foissner, 1978

Family Cyrtolophosididae Stokes, 1888

Genus *Cyrtolophosis* Stokes, 1885

Cyrtolophosis minor² Vuxanovici, 1963

Distribution. JAMAICA: (Dunthorn *et al.* 2012).

Cyrtolophosis mucicola Stokes, 1885

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad); (Foissner *et al.* 2003). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Genus *Pseudocyrtolophosis* Foissner, 1980

Pseudocyrtolophosis alpestris Foissner, 1980

Distribution. BRAZIL: (Foissner *et al.* 2003). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: Ixtlán de Juárez (Durán-Ramírez *et al.* 2015), (To); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016); North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Incertae sedis in family Cyrtolophosidae

Genus *Plesiocaryon* Foissner, Agatha, & Berger, 2002

Plesiocaryon elongatum (Schewiakoff, 1892) Foissner, Agatha & Berger, 2002

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Family Platyphryidae de Puytorac, Perez-Paniagua & Perez-Silva, 1979

Genus *Platyphrya* Kahl, 1926

Platyphrya bromelicola^{1,2} Foissner, 2008

Distribution. BRAZIL: (Dunthorn *et al.* 2012; Foissner 2016); Rio de Janeiro (Foissner 2016). JAMAICA: (Foissner 2016); Saint Thomas, at the eastern tip of Jamaica, near the villages of Golden Grove and Rowlandsfield (Foissner & Wolf 2009). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th).

Platyphrya macrostoma Foissner, 1980

Distribution. VENEZUELA: North border of the Henri Pittier National Park, surroundings of the village of Choroni (Foissner 2016), (Ts).

Platyphrya vorax Kahl, 1926

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003).

Class Prostomatea Schewiakoff, 1896

Order Prorodontida Corliss, 1974

Family Colepidae Ehrenberg, 1838

Genus *Coleps* Nitzsch, 1827

Coleps hirtus (Müller, 1786) Nitzsch, 1827

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Holophryidae Perty, 1852

Genus *Holophrya* Ehrenberg, 1831

Holophrya teres (Ehrenberg, 1833) Foissner, Berger & Kohmann, 1994

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Plagiocampidae Kahl, 1926

Genus *Plagiocampa* Schewiakoff, 1893

Plagiocampa rouxi Kahl, 1926

Distribution. BRAZIL: (Foissner *et al.* 2003); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Urotrichidae Small & Lynn, 1985

Genus *Bursellopsis* Corliss, 1960

Bursellopsis spumosa (Schmidt, 1920) Corliss, 1960

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Urotricha* Claparède & Lachmann, 1859

Urotricha farcta Claparède & Lachmann, 1859

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Class Plagiopylea Small & Lynn, 1985

Order Odontostomatida Sawaya, 1940

Family Discomorphellidae Corliss, 1960

Genus *Discomorphella* Corliss, 1960

Discomorphella pectinata (Levander, 1894) Corliss, 1960

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Epalkellidae Corliss, 1960

Genus *Saprodnium* Lauterborn, 1908

Saprodnium dentatum (Lauterborn, 1901) Lauterborn, 1908

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Order Plagiopylida Jankowski, 1978

Family Plagiopylidae Schewiakoff, 1896

Genus *Plagiopyla* Stein, 1860

***Plagiopyla nasuta* Stein, 1860**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Class Oligohymenophorea de Puytorac *et al.* 1974

Subclass Hymenostomatia Delàge & Hérouard, 1896

Order Tetrahymenida Fauré-Fremiet in Corliss, 1956

Family Glaucomidae Corliss, 1971

Genus *Bromeliophrya* Foissner, 2003

***Bromeliophrya brasiliensis*^{1,2} Foissner, 2003**

Distribution. BRAZIL: (Dunthorn *et al.* 2012; Foissner *et al.* 2003); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad); Surroundings of the Village of Praia do Forte, about 81 km North of the town of Salvador, Bahia (Foissner 2003a), (As). ECUADOR: (Foissner *et al.* 2003). JAMAICA: (Dunthorn *et al.* 2012). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2019), (Th); Dos Lagunas, near Village of Tzsiscaco (ps), (Ch, Tg, Tm, Ws); El Tegolome, near the town of Tlanchinol (ps), (Ti); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2019), (Te, Ts); (ps), (Cs, Pv, Te); Village El Cerezal, near Santa Catarina Ixtapejí (ps), (To); (Durán-Ramírez *et al.* 2016).

***Bromeliophrya quadristicha*¹ Foissner & Stoeck, 2013**

Distribution. DOMINICAN REPUBLIC: Botanical Garden on the Pico Isabel de Torres, 800 m high mountain on the outskirts of the town of Puerto Plata (Foissner & Stoeck 2013). JAMAICA: Northern slope of the Blue Mountains, surroundings of the village of Silver Hill (Foissner & Stoeck 2013).

Genus *Glaucoma* Ehrenberg, 1830

***Glaucoma reniforme* Schewiakoff, 1892**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

***Glaucoma scintillans* Ehrenberg, 1830**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Bromeliophryidae Foissner, 2003

Genus *Glaucomides* Foissner, 2013

***Glaucomides bromelicola*^{1,2} Foissner, 2013**

Distribution. CHILE: (Foissner 2013). DOMINICAN REPUBLIC: (Dunthorn *et al.* 2012; Weisse *et al.* 2013a);

Botanical Garden on the Pico Isabel de Torres, 800 m high mountain on the outskirts of the town of Puerto Plata (Foissner 2013). ECUADOR: (Foissner 2013). JAMAICA: (Foissner 2013); (Dunthorn *et al.* 2012), (Ap, Cb, Gm, Hi, Hp, Hr, Hn, Hs, Hu, Ts, Vs). MEXICO: Coffee plantation Arcos Vegas and Rincón de Yeguas, Tuzamapan (Durán-Ramírez *et al.* 2019), (Ab, Am); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscão (ps), (Ch, Tg, Tm, Ws); El Tegolome, near the town of Tlanchinol (ps), (Ti, Tm, Ts); La Joya, Acajete (Durán-Ramírez *et al.* 2019), (Ta, Ts, Ty); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Durán-Ramírez *et al.* 2019), (Pv, Te, Tm, Ts); (ps), (Cs, Te, Tm, Ts); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Cs, Th); Tlacuitlapa, Jalcomulco (Durán-Ramírez *et al.* 2019), (Ab, Pg); Village El Cerezal, near Santa Catarina Ixtépeji (ps), (To); (Foissner 2013). PERU: (Foissner 2013). VENEZUELA: (Foissner 2013).

Family Tetrahymenidae Corliss, 1952

Genus *Lambornella* Keilin, 1921

Lambornella trichoglossa^{1,2} Foissner, 2003

Distribution. BRAZIL: (Dunthorn *et al.* 2012; Foissner *et al.* 2003); Garapia River, Rio Grande do Sul (Malfatti 2019), (Vi); Maquiné River basin, Rio Grande do Sul (Malfatti 2019), (Vg); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad); Pró-Mata de São Francisco de Paula, Rio Grande do Sul (Malfatti 2019), (Vf, Vy); Surroundings of the Village of Praia do Forte, about 81 km North of the town of Salvador, Bahia (Foissner 2003b), (As); ECUADOR: (Foissner *et al.* 2003). DOMINICAN REPUBLIC: (Foissner *et al.* 2003); North slope of the Cordillera Central, in the surroundings of the waterfall Salto de Jimenoa (Foissner 2003b); Santiago de los Caballeros (Foissner 2003b). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Ixtlán de Juárez (Durán-Ramírez *et al.* 2015), (To).

Genus *Tetrahymena* Furgason, 1940

Tetrahymena rostrata (Kahl, 1926) Corliss, 1952

Distribution. BRAZIL: (Foissner *et al.* 2003). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th).

Family Turaniellidae Didier, 1971

Genus *Colpidium* Stein, 1860

Colpidium colpoda (Losana, 1829) Stein, 1860

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Colpidium kleini Foissner, 1969

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Dexiostoma* Jankowski, 1967

Dexiostoma campylum (Stokes, 1886) Jankowski, 1967

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subclass Peniculia Fauré-Fremiet in Corliss, 1956

Order Peniculida Fauré-Fremiet in Corliss, 1956

Family Frontoniidae Kahl, 1926

Genus *Frontonia* Ehrenberg, 1838

***Frontonia depressa* (Stokes, 1886) Kahl, 1931**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

***Frontonia leucas* (Ehrenberg, 1833) Ehrenberg, 1838**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

***Frontonia pusilla* Fan *et al.* 2013**

Distribution. MEXICO: Coastal Research Center CICOLMA (Durán-Ramírez *et al.* 2019), (Bp).

Family Lembadionidae Jankowski in Corliss, 1979

Genus *Lembadion* Pery, 1849

***Lembadion bullinum* (Müller, 1786) Perty, 1849**

Distribution. BRAZIL: Bracuhy Port, Angra dos Reis (Esteves & Silva-Neto 1996); Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

***Lembadion lucens* (Maskell, 1887) Kahl, 1931**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Parameciidae Dujardin, 1840

Genus *Paramecium* Müller, 1773

***Paramecium caudatum* Ehrenberg, 1833**

Distribution. BRAZIL: Garapia River, Rio Grande do Sul (Malfatti 2019), (Vi); Maquiné River basin, Rio Grande do Sul (Malfatti 2019), (Vg); Pró-Mata, in São Francisco de Paula, Rio Grande do Sul (Malfatti 2019), (Vf, Vy). COLOMBIA: (Paz 1980), (Gs).

***Paramecium multimicronucleatum* Powers & Mitchell, 1910**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014a, b, 2015), (Ad).

***Paramecium putrinum* Claparède & Lachmann, 1859**

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Order Urocentrida Jankowski, 1980

Family Urocentridae Claparède & Lachmann, 1858

Genus *Urocentrum* Nitzsch, 1827

Urocentrum turbo (Müller, 1786) Nitzsch, 1827

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Subclass Peritrichia Stein, 1859

Order Sessilida Kahl, 1933

Family Epistylididae Kahl, 1933

Genus *Campanella* Goldfuss, 1820

Campanella umbellaria (Linnaeus, 1758) Goldfuss, 1820

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Epistylis* Ehrenberg, 1830

Epistylis plicatilis Ehrenberg, 1831

Distribution. MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab).

Genus *Orborhabdostyla* Foissner, Blake, Wolf, Breiner & Stoeck, 2009

Orborhabdostyla bromelicola^{1,2} Foissner, Blake, Wolf, Breiner & Stoeck, 2009

Distribution. ECUADOR: Esmeraldas, underneath Alto Tambo (Foissner *et al.* 2009), (Gm). JAMAICA: (Dunthorn *et al.* 2012), (Gu).

Family Vorticellidae Ehrenberg, 1838

Genus *Pseudovorticella* Foissner & Schiffmann, 1975

Pseudovorticella bromelicola¹ Foissner, Blake, Wolf, Breiner & Stoeck, 2009

Distribution. BRAZIL: Parque Estadual do Ibitipoca, Minas Gerais (Costa-Muniz 2019), (Af, Nf, Ni, Nm, No, Vb, Vf, Vh, Vp, Wg). COSTA RICA: Tropic station La Gamba (Foissner *et al.* 2009), (Gz).

Genus *Vorticella* Linnaeus, 1767

Vorticella convallaria² Linnaeus, 1758

Distribution. JAMAICA: (Dunthorn *et al.* 2012).

Vorticella gracilis² Dujardin, 1841

Distribution. COSTA RICA: (Dunthorn *et al.* 2012; Foissner *et al.* 2009). JAMAICA: (Dunthorn *et al.* 2012).

Genus *Vorticellides* Foissner, Blake, Wolf, Breiner & Stoeck, 2009

***Vorticellides aquadulcis*²** (Stokes, 1887) Foissner, Blake, Wolf, Brenier & Stoeck, 2009

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná [recorded as *Vorticella aquadulcis*] (Buosi *et al.* 2014b, 2015), (Ad). COSTA RICA: (Foissner *et al.* 2009). MEXICO: Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (Dunthorn *et al.* 2012).

***Vorticellides astyliformis*²** (Foissner, 1981) Foissner, Blake, Wolf, Brenier & Stoeck, 2009

Distribution. COSTA RICA: (Dunthorn *et al.* 2012; Foissner *et al.* 2009). VENEZUELA: South margin of the Henri Pittier National Park Biological Station Rancho Grande [recorded as *Vorticella astyliformis*] (Foissner 2016).

Subclass Scuticociliatia Small, 1967

Order Philasterida Small, 1967

Family Cinetochilidae Perty, 1852

Genus *Cinetochilum* Perty, 1849

Cinetochilum margaritaceum (Ehrenberg, 1830) Perty, 1852

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003).

Genus *Sathrophilus* Corliss, 1960

Sathrophilus muscorum (Kahl, 1931) Corliss, 1960

Distribution. BRAZIL: (Foissner *et al.* 2003). MEXICO: Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th). VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Family Loxocephalidae Jankowski, 1964

Genus *Dexiotricha* Stokes, 1885

Dexiotricha granulosa (Kent, 1881) Foissner, Berger & Kohmann, 1994

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). ECUADOR: (Foissner *et al.* 2003).

Family Philasteridae Kahl, 1931

Genus *Kahlilembus* Grolière & Couteaux, 1984

Kahlilembus attenuatus (Smith, 1897) Foissner, Berger & Kohmann, 1994

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Genus *Philasterides* Kahl, 1931

Philasterides armatus (Kahl, 1926) Kahl, 1931

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Uronematidae Thompson, 1964

Genus *Homalogastra* Kahl, 1926

Homalogastra setosa Kahl, 1926

Distribution. VENEZUELA: South margin of the Henri Pittier National Park, Biological Station Rancho Grande (Foissner 2016).

Order Pleuronematida Fauré-Fremiet in Corliss, 1956

Family Calyptotrichidae Small & Lynn, 1985

Genus *Calyptotricha* Phillips, 1882

Calyptotricha lanuginosa (Penard, 1922) Wilbert & Foissner, 1980

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Ctedoctemataidae Small & Lynn, 1985

Genus *Ctedoctema* Stokes, 1884

Ctedoctema acanthocryptum Stokes, 1884

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Family Cyclidiidae Ehrenberg, 1838

Genus *Cyclidium* Müller, 1773

Cyclidium glaucoma Müller, 1773

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad). DOMINICAN REPUBLIC: (Foissner *et al.* 2003). ECUADOR: (Foissner *et al.* 2003). MEXICO: Biocultural Reserve Kaxil Kiuic, near Oxkutzcab (ps), (Ab); Coffee plantation La Onza, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec (Durán-Ramírez *et al.* 2015), (Th); Dos Lagunas, near Village of Tzsiscaco (ps), (Ch, Tg, Tm, Ws); El Tegolome, near the town of Tlanchinol (ps), (Ti, Tm, Ts); Reserve of the Biosphere Chamela-Cuixmala (Durán-Ramírez & Mayén-Estrada 2018), (Bk, Td, Tp, Tr); Santuario del Bosque de Niebla, near Xalapa (Durán-Ramírez *et al.* 2015), (Th); (ps), (Te); surroundings of Reserva Azul, near the town of Cuetzalan (ps), (Th); Village El Cerezal, near Santa Catarina Ixtepeji (ps), (To).

Cyclidium heptatrichum Schewiakoff, 1893

Distribution. BRAZIL: Paraná River between the Nupelia's Field Station and the district of Porto São José, São Pedro do Paraná (Buosi *et al.* 2014b, 2015), (Ad).

Genus *Protocyclidium* Alekperov, 1993

Protocyclidium muscicola (Kahl, 1931) Foissner, Agatha & Berger, 2002

Distribution. BRAZIL: [recorded as *Cyclidium muscicola*] (Foissner *et al.* 2003). DOMINICAN REPUBLIC: [recorded as *Cyclidium muscicola*] (Foissner *et al.* 2003). ECUADOR: [recorded as *Cyclidium muscicola*] (Foissner *et al.* 2003). MEXICO: Coffee plantation La Onza, near Coatepec [recorded as *Cyclidium muscicola*] (Durán-Ramírez *et al.* 2015), (Th); Coffee plantation Virginia Armand, near Coatepec [recorded as *Cyclidium muscicola*] (Durán-Ramírez *et al.* 2015), (Th).

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DISCUSIÓN GENERAL Y CONCLUSIONES

Las bromeliáceas son un elemento conspicuo de la flora neotropical siendo relevantes desde el punto de vista ecológico por su papel como microambientes. Se distribuyen en todos los países de América excepto Canadá, y México es un centro de especiación para esta familia, en donde se han identificado 422 especies de bromelias y ocho taxones infraespecíficos (Espejo-Serna & López-Ferrari, 2018), de las cuales 40% (180 aproximadamente) presentan morfología tipo tanque; de éstas, solo en 27 especies se han estudiado los ciliados que habitan dentro de ellas (Durán-Ramírez & Mayén-Estrada, 2018; Durán-Ramírez *et al.*, 2015, 2019, 2020), lo cual denota la falta de estudios ciliológicos en este tipo de ambientes.

Dentro de una bromelia, se pueden reconocer tres hábitats para los ciliados: (1) la columna de agua que se deposita entre las hojas y que dan lugar a la formación del tanque, (2) los detritos acumulados en el fondo del tanque y entre las bases de las hojas coalescentes de la planta y (3) como epibiontes sobre el cuerpo de invertebrados (Foissner *et al.*, 2003). En este estudio, los ciliados se identificaron en la columna de agua y entre los detritos. Una aportación dada a conocer en el presente estudio fue que las bromelias sin morfología tanque que no forman una fitotelma, como las del género *Bromelia* del bosque tropical caducifolio de la Reserva de la Biósfera Chamela Cuixmala y de la vegetación de dunas costeras en Veracruz, representan microhábitats donde también se establecen comunidades de ciliados. Las especies de estas comunidades, muchas de las cuales son comunes en suelos, colonizaron bromelias de este género utilizando los recursos disponibles como la materia orgánica húmeda acumulada entre las bases de las hojas, raíces, así como entre los remanentes de las inflorescencias en descomposición (Durán-Ramírez & Mayén-Estrada, 2018; Durán-Ramírez *et al.*, 2019).

Recientemente, se han publicado algunos inventarios sobre la presencia de ciliados en especies de bromelias de Brasil, Ecuador, Jamaica, República Dominicana y Venezuela y datos aislados se han mencionado a partir de bromelias de Chile, Colombia, Costa Rica y Perú (Buosi *et al.*, 2014, 2015; Durán-Ramírez *et al.*, 2015; Dunthorn *et al.*, 2012; Foissner, 2016; Foissner *et al.*, 2003). En México, el número de especies de ciliados de bromelias previamente registrado, incluyendo las que se dan a conocer en la presente tesis, equivalen casi al 6% del total de especies documentadas en el país (Mayén-Estrada *et al.*, 2019).

De manera comparativa, se observó que el número de especies de ciliados identificados para las bromelias de la Reserva de la Biósfera de Chamela Cuixmala (Durán-Ramírez & Mayén-Estrada,

2018), así como en las poblaciones de bromelias distribuidas a lo largo de un gradiente de elevación del Centro de Veracruz (Durán-Ramírez *et al.*, 2019) fue menor en comparación con las 61 especies registradas en el año 2009 en una población de *Tillandsia heterophylla* en plantaciones de café y remanentes de bosque mesófilo de montaña (Durán-Ramírez *et al.*, 2015); valores más bajos de riqueza específica (19) fueron reportados por Paz (1980) en una población de bromelias epífitas del género *Guzmania* del Chocó en Colombia. En contraste, valores más altos de riqueza específica fueron obtenidos en una población de *Aechmea distichantha* por Buosi *et al.* (2014, 2015) a lo largo de la ribera del Río Paraná al sur de Brasil, cuya comunidad de ciliados estuvo conformada por 92 especies. Es constante que en las bromelias, las clases de ciliados Colpodea, Oligohymenophorea y Spirotrichea son las que agrupan al mayor número de especies.

Previamente se había documentado que algunos géneros de amplia distribución y que son frecuentes en cuerpos de agua dulce, no colonizan bromelias, como lo es *Paramecium* Müller, 1773, *Frontonia* Ehrenberg, 1838, *Glaucoma* Ehrenberg, 1830 y *Trithigmostoma* Jankowski, 1967, ya que hasta hace poco, ninguna especie de estos géneros había sido registrada en bromelias (Dunthorn *et al.*, 2012), pero Buosi *et al.* (2014) identificaron a *Paramecium multimicronucleatum* en *Aechmea distichantha* al sur de Brasil. En el presente estudio, se observaron dos especies de *Frontonia* pertenecientes a la clase Oligohymenophorea, habitando en bromelias sin morfología tipo tanque y cuya dieta está constituida por detritos y esporas que se acumulan en las bromelias.

Leptopharynx bromeliophilus y *Gonostomum bromelicola*, especies de las clases Nassulida y Spirotrichea respectivamente, tienen una distribución restringida a México y las Antillas, mientras que *Cotterillia bromelicola* (Spirotrichea) se restringe a bromelias de México y a algunos ambientes terrestres en Costa Rica (Foissner & Stoeck, 2011). Aún más restringida, es la distribución de *Paraoxytricha quadrinucleata* (Spirotrichea), descrita en una población de *Tillandsia heterophylla*, cuya localidad tipo se encuentra en Xalapa, Veracruz (Foissner, 2016). Otras especies que no son exclusivas de bromelias, pero que hasta ahora sólo se han registrado en el Neotrópico, son *Paracolpoda lajacola* (Colpodida), la cual se distribuye solo en la porción del hemisferio Norte, desde México hasta Venezuela (Foissner, 2016), y *Bresslauides terricola*, un colpódido que también habita en otros continentes, pero en el Neotrópico, ha mostrado una distribución restringida a la porción del hemisferio Norte. Altitudinalmente, resalta la distribución de *Fragmocirrus espeletiae* (Spirotrichea), cuyo hábitat en donde se describió se encuentra por encima de los 4,000 metros (Foissner, 2000) y se observó únicamente en bromelias del bosque mesófilo de montaña en Hidalgo a una elevación de 1400 metros de altitud (Durán-Ramírez *et al.*, 2020).

Los ambientes donde se han registrado los ciliados en las bromelias incluyen parques nacionales y reservas de la biosfera con distintos tipos de vegetación como el bosque tropical caducifolio, bosque mesófilo de montaña, bosque tropical perennifolio y encinares; también sobre los márgenes de ríos, plantaciones de café y algunos jardines botánicos (Buosi *et al.*, 2014, 2015; Durán-Ramírez *et al.*, 2015; Foissner, 2016; Foissner *et al.*, 2003). Sin embargo, existen hábitats propicios tanto en México como en una veintena más de países neotropicales donde se distribuyen las bromeliáceas los cuales aún no han sido considerados.

Los estudios ecológicos de ciliados en bromelias son escasos, pero se han abordado algunos aspectos y algunas variables ambientales y fisicoquímicas que posiblemente influyen sobre la composición de la comunidad, tal y como lo es en primer lugar, la presencia de agua acumulada al interior de las plantas con morfología tipo tanque. Buosi *et al.* (2014) demostraron que la cercanía de las bromelias a cuerpos de agua dulce como ríos, propicia que ciertas especies de ciliados dulceacuícolas sean capaces de colonizarlas. Respecto a la estacionalidad, algunos trabajos refieren que la riqueza específica de ciliados de las bromelias es mayor durante la temporada seca, mientras que otros han documentado que es durante la temporada húmeda (Buosi *et al.*, 2014, 2015; Durán-Ramírez *et al.*, 2015; Foissner *et al.*, 2003); también se ha documentado que la temperatura del agua y la altitud sobre el nivel del mar son dos variables que operan sobre la composición de la comunidad de ciliados que a su vez, a nivel local puede ser diferente con respecto al tipo de vegetación en donde habitan las bromelias (Durán-Ramírez *et al.*, 2019).

La presencia de ciliados en bromelias puede explicarse también debido a la alternancia entre períodos de sequía y humedad, al aislamiento parcial respecto al medio circundante, sobre todo en el dosel del bosque y a la competencia intra e interespecífica a la que están sometidos. La existencia de especificidad ciliado-bromelia, es aparentemente inexistente (Dunthorn *et al.*, 2012), y por ello la identidad taxonómica de las bromelias no es determinante en la composición de la comunidad de ciliados. Para los ciliados, la relevancia de las bromelias radica en que no hay otro microhábitat con las mismas características, en donde puedan establecerse en tiempo y espacio, e incluso obtener resguardo para mantener poblaciones viables. De manera precisa, se establece que la especificidad que existe es de tipo ecológico, es decir, que las bromelias representan un microhábitat temporal favorable, lo cual cobra mayor relevancia si se considera el hecho de que se trata de un tipo de microhábitat que solo se halla en la Región Neotropical.

Además de bromelias, existen pocas evidencias de la presencia de ciliados en otros puntos del dosel en los bosques tropicales. Bamforth (2007) identificó alrededor de 50 especies de ciliados en el

suelo suspendido formado por musgos en ramas de árboles de un bosque tropical en Puerto Rico, de las cuales, coincidieron nueve especies cosmopolitas observadas en las bromelias del presente estudio, pero ninguna de las consideradas habitantes exclusivas de las bromelias, fueron observadas en este biotopo.

Con los resultados de la presente tesis, se amplía el conocimiento de las comunidades de ciliados en distintas especies de bromelias, principalmente del género *Tillandsia* circunscritas a esta región del Neotrópico, considerando un gradiente de elevación, así como distintos tipos de vegetación característicos de las zonas de montaña del centro y sur de México y bosques tropicales a elevaciones bajas de la Península de Yucatán y de la vertiente del Pacífico. Se concluye que por su distribución restringida al Neotrópico y sus características como microambientes, las bromeliáceas son un modelo de estudio para continuar abordando aspectos sobre diversidad, ecología y distribución de los ciliados.

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