



Free-living ciliates from epiphytic tank bromeliads in Mexico

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Abstract

The ciliate diversity of Mexican bromeliads is poorly known. We studied the ciliate community of two species of epiphytic tank bromeliads from 48 individuals of *Tillandsia heterophylla* and four of *T. prodigiosa*. The bromeliads occurred on over 22 tree host species. Samples were collected during 2009 and 2010 in a mountain cloud forest and in two coffee plantations and in a pine–oak forest. The ciliates were identified in live and protargol preparations. We recorded 61 ciliate species distributed in 39 genera grouped in eight classes. Ten species were frequent in the 52 samples (20 ± 3.2) and *Leptopharynx bromeliophilus* was the most frequent recorded in 25 samples. Thirty-three species are new for the fauna of Mexico, 24 species have been recorded for the first time in tank bromeliads. The classes Spirotrichea, Oligohymenophorea and Colpodea presented the highest number of species, 16, 14, and 12, respectively. *Colpoda* was the most species-rich genus being present with six species. A low similarity between areas and seasons was obtained with Jaccard's index. We conclude that the two bromeliads species host a rich ciliate diversity whose knowledge contributes to the question of ciliate distribution and specifically, in tank bromeliads.

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Introduction

Members of the family Bromeliaceae dominate the epiphytic vascular flora of Neotropical forests (Benzing 1990). They increase the structural complexity of the canopy because of the additional resources they provide to the fauna, playing an important role in productivity, water capture and nutrient cycling (Nadkarni 1986; Nadkarni and Matelson

1989). Tank bromeliads capture rain water and organic matter between the axes of their leaves (Frank and Lounibos 1987). These phytotelmata can be ephemeral or may contain up to 45 l of water which has a pH ranging from 4 to 7 (Guimaraes-Souza et al. 2006; Zahl 1975). Temperature is also an important factor that determines the presence of the biota living in the tanks (Laessle 1961). Haubrich et al. (2009) found that microenvironmental conditions can considerably vary in a matter of hours within the tank.

There are 3086 bromeliad species distributed mainly in tropical America, from the south of the United States to south Argentina (Frank et al. 2004; Luther 2006). In Mexico, 342

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species have been reported (Espejo-Serna et al. 2004); the states having the greatest diversity are Oaxaca (135 species), Chiapas (121 species) and Veracruz (91 species). The genus *Tillandsia* is relevant because about one-third of its species is native to North America (Padilla 1973) and Mexico is considered as center of their diversification (Espejo-Serna and López-Ferrari 1998).

Richardson (1999) showed that the macroinvertebrate fauna inhabiting bromeliads can be considered as an indicator of local diversity. Tank bromeliads promote aquatic food web diversity in Neotropical forests because the environmental conditions can differ from one plant to another (Brouard et al. 2012). Carrias et al. (2001) investigated the importance of the protozoans in this microenvironment and concluded that they are key players because they stimulate the degradation of accumulated organic matter and they proposed a positive correlation between protozoan abundance and microinvertebrates, such as rotifers, copepods and mosquito larvae.

Ciliates are protists that constitute an important component of the ecosystems because they participate actively in nutrient cycling and control bacterial populations (Brunberg-Nielsen 1968; Caron 1991). According to Lynn (2008), there are around 8000 species of ciliates known worldwide, 959 of which have been recorded in Mexico (Mayén-Estrada et al. 2014). However, Foissner et al. (2008) suggested that around 80% of global free-living ciliate species diversity remains undescribed.

The ciliate species present in tank bromeliads have received little attention, although there are records from Central America, South America, some West Indian islands and the Dominican Republic (Carrias et al. 2001; Dunthorn 2005; Foissner, 2003a,b, 2013; Foissner et al. 2003; Foissner and Stoeck 2013; Laessle 1961; Maguire 1971; Omar and Foissner 2011). New species have been discovered in tank bromeliads by Dunthorn (2005), Foissner (2003a,b, 2006), Foissner et al. (2003, 2008). Since there are about 3000 bromeliad species with distinct habitats and morphologies, Foissner et al. (2003) suggested that hundreds of new ciliate species may await discovery. Dunthorn et al. (2012) mentioned that many of such species are restricted to the Neotropics, and that this type of phytotelmata provides evidence for the speciation and endemism of some bromeliad ciliates in Neotropics. Generally, the ciliate communities of tank bromeliads comprise a mixture of new species and taxa from freshwater, moss and soil (Foissner et al. 2003). There are two main categories of free-living ciliates that inhabit bromeliads: those that inhabit the water column and the mud and those that live as epibionts attached to invertebrates (Foissner et al. 2003). Water is probably the most important environmental factor affecting the presence of ciliates in bromeliads (Foissner 2005). Several free living species possess the ability to form resting cysts or to change their morphology, particularly their cell size and oral structure in order to adapt from feeding on bacteria to feeding on larger prey organisms such as other protists and microinvertebrates (Foissner et al. 2003); the same authors suggested that

competition and isolation play an important role in the process of speciation and endemism of some of the bromeliad ciliates species. Thus, the tank of a bromeliad constitutes a highly competitive microecosystem due to the decreasing space and resources during dry periods (Foissner et al. 2003).

Knowledge of the diversity and ecology of ciliates that inhabit bromeliads in Mexico is sparse although some notes have been made of ciliates from *Tillandsia heterophylla* by Dunthorn et al. (2012), Foissner (2010), Foissner and Stoeck (2011), Foissner et al. (2011) and Omar and Foissner (2011). There are, however no records of bromeliad ciliates from Oaxaca. The present study aims to increase knowledge of ciliates inhabiting species of epiphytic bromeliads from temperate and tropical environments of Mexico.

Material and Methods

Samples of water and mud were collected from the tanks of two endemic bromeliads growing at four areas in Mexico (Fig. 1). Samples 1–48 were from *T. heterophylla* and were collected during the dry and wet seasons of 2009; samples 49–52 were from *T. prodigiosa* and were collected during the dry season of 2010.

- (1) Samples 1–16: Santuario de Bosque de Niebla, Xalapa, Veracruz, Mexico (N96°56'W19°30'; 1250 m a.s.l.). Protected natural area of 43.5 ha with remnants of mountain cloud forest and a secondary forest surrounded by urban areas and coffee plantations.
- (2) Samples 17–32: Coffee plantation “La Onza”. This is an agroecosystem that is located in Las Puentes Village, W Coatepec, Veracruz, Mexico (N19°20'W96°48', 1100 m a.s.l.). It is an 8 ha area where agroforestry is practiced with coffee production since 200 years, although it now supports a variety of crops including coffee and bananas. Its main characteristics are some native arboreal elements of the mountain cloud forest, with the presence of exotic tree species that provide shade for the coffee and banana plantations. The soil is mainly fertilized with organic wastes from the coffee production and occasionally with agrochemicals.
- (3) Samples 33–48. Coffee plantation “Virginia Armand”. This is an agroecosystem located SE of Coatepec, Veracruz, Mexico (N19°21'W96°47'; 1200 m a.s.l.). It is a coffee land of 20 ha but partially covered with *Inga* trees that provide shade for the coffee shrubs; there are also some native floristic elements. The use of agrochemicals is unknown. The area is surrounded by sugar cane and other coffee plantations.
- (4) Samples 49–52. Slope with pine–oak forest in the Sierra Juárez, Ixtlán de Juárez, Oaxaca, Mexico (N17°18'W96°28'; 1950 m a.s.l.). The vegetation is a secondary forest and a reforested area with pine–oak trees, viz. *Pinus pseudostrobus* and *Quercus* spp.

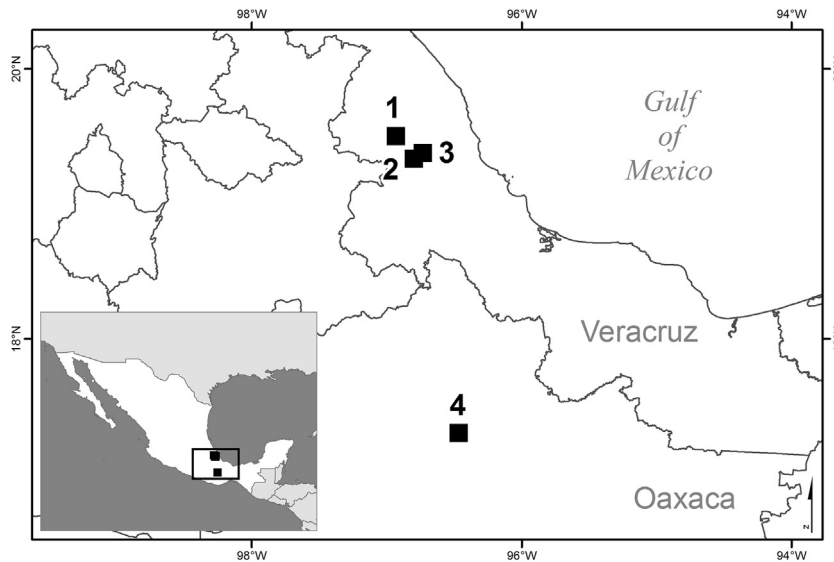


Fig. 1. Location of Mexico collection areas 1–4. Area 1. Santuario de Bosque de Niebla, Xalapa, Veracruz. Area 2: Coffee plantation La Onza, Coatepec, Veracruz. Area 3. Coffee plantation Virginia Armand, Coatepec Veracruz. Area 4. Pine-oak forest in the Sierra Juárez, Ixtlán de Juárez, Oaxaca.

Samples were collected with a 60 ml plastic syringe connected to a crystal tube. Each sample comprised a combination of water and mud accumulated in the rosette of the plant. The samples were deposited individually in plastic vials. Because the bromeliads are epiphytic, rope-climbing methods were employed in collecting samples from bromeliads growing more than 2 m above the ground (Flores-Palacios and García-Franco 2001). None of the plants were removed from their substrate as suggested by Jocque et al. (2010). The distance above ground level where bromeliads were growing was measured and also all water volume contained in the plants were measured; water temperature and pH were measured with a Barnant 20[®] Digital pH/mV/ORP Meter 559-3800 Serial M96006308. Samples were transported and maintained under laboratory conditions according to the procedure of Foissner et al. (2003).

Samples were checked daily for four weeks after sampling. Occasionally, 20 ml of aliquots of distilled water were added in order to keep the samples hydrated. Ciliates were cultured in Petri dishes with either a combination of water from the environment and some milliliters of mineral water Eau de Volvic[®] enriched with wheat grains to stimulate the growth of bacteria. In some cases, flagellates and other ciliates were also added as food (Foissner et al. 2003). Ciliates were observed *in vivo* using bright field, phase contrast, and differential interference contrast (DIC). In order to reveal the infraciliature and other cytological structures, we applied supravital staining (green methyl-pyronin) and silver impregnation techniques following the procedures of Foissner (1991). Some specimens were also examined by scanning electron microscopy (SEM) following the protocol of Foissner (1991) and employing a Cambridge Stereoscan 250. Genera and species identifications were made according to Berger (1999, 2006), Corliss (1979), Czapik (1968),

Foissner (1982, 1993, 2003b, 2010), Foissner et al. (1992, 1994, 2002, 2003), Foissner and Stoeck (2011), Foissner and Wolf (2009), Foissner and Xu (2007), Grasse (1994), Kreutz and Foissner (2006), Lee et al. (1985), Oertel et al. (2009) and Omar and Foissner (2011).

To compare the water volume contained in the bromeliad tanks and the distance above the ground where plants were growing, we applied a Kruskal–Wallis One Way Analysis of Variance (H), (SigmaStat 3.5). For water temperature and pH, only the mean and standard deviation were calculated. Similarity between areas and seasons was evaluated with Jaccard index ($I_j = c/[a + b - c]$), where *a* is the number of species in the area *A*, *b* is the number of species in the area *B*, and *c* is the number of species shared between *A* and *B* (Moreno 2001; MVSP 3.22 Kovach Computing Services).

Results

The bromeliads sampled contained 8 to 800 ml (153.3 ± 155.6 ; $H = 10.4$, $P < 0.05$) water; only one individual was dry. All plants were epiphytic, presented a similar size and were located almost at the same distance above ground level (3.5 ± 2.1 ; $H = 1.7$, $P > 0.5$). The water temperature was $19\text{--}29^\circ\text{C}$ (23.5 ± 2.1), and the pH was $4.8\text{--}6.9$ (6.1 ± 0.5). This acidic trend of the water of the bromeliad tanks results in a slow decomposition of the organic matter (Foissner et al. 2003). The bromeliads occurred on over 22 tree host species (Table 1).

On average, each of the 52 fresh samples contained $6.9 (\pm 4.7)$ ciliate species, and each species was present in an average of 5.9 samples. The minimum number of species per sample was 0 (sample 16) and the maximum was 18 species (sample 27). Most samples (42 or 80.7%) contained 1–10

Table 1. Ciliates species from the bromeliads *Tillandsia heterophylla* and *T. prodigiosa* found in samples 1–52¹.

Species ²											
	1	2	3	4	5	6	7	8	9	10	11
<i>Acineta</i> sp.	–	–	–	–	–	–	–	+	–	–	–
<i>Arcuospathidium namibiense tristicha</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Arcuospathidium cultriforme scalpriforme</i>	–	+	–	–	–	–	–	–	–	–	–
<i>Blepharisma steini</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Bromeliothrix metopoides</i>	–	+	–	–	–	–	–	–	–	–	–
<i>Chilodonella uncinata</i>	+	+	+	+	+	–	–	–	–	–	–
<i>Colpoda cucullus</i>	–	+	–	–	–	–	–	–	–	–	–
<i>Colpoda henneguyi</i>	–	+	–	–	–	–	–	–	–	+	–
<i>Colpoda inflata</i>	–	–	+	–	–	–	–	–	–	–	–
<i>Colpoda lucida</i>	+	–	–	+	–	–	–	+	–	–	–
<i>Colpoda maupasi</i>	–	–	–	+	–	+	–	–	–	–	–
<i>Colpoda steinii</i>	–	–	+	+	–	–	–	–	–	+	–
<i>Coriplites proctori</i>	+	–	+	+	–	–	–	–	–	–	–
<i>Cotterillia bromelicola</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Ctedoctema</i> sp.	–	–	–	–	–	–	–	–	–	–	–
<i>Cyclidium glaucoma</i>	+	+	+	+	–	–	+	+	+	+	–
<i>Cyclidium muscicola</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Cyrtohymena quadrinucleata</i>	–	–	–	–	–	–	–	–	–	+	–
<i>Cyrtolophosis mucicola</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Drepanomonas pauciciliata</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Drepanomonas revoluta</i>	+	–	–	–	–	–	–	–	–	–	–
<i>Euplotes</i> sp.	–	–	–	–	–	–	–	–	–	–	–
<i>Frontonia depressa</i>	+	+	–	–	–	–	+	+	–	–	–
<i>Gastrostyla</i> (undescribed sp.)	–	–	–	–	–	–	–	–	–	–	–
<i>Glaucomides bromelicola</i>	+	–	–	+	–	–	+	–	+	+	+
<i>Gonostomum affine</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Gonostomum kuehnelti</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Halteria grandinella</i>	+	–	+	+	–	–	+	+	–	–	–
<i>Holosticha muscorum</i>	–	–	+	+	–	–	–	–	–	–	–
<i>Lambornella</i> (undescribed sp.)	+	+	+	+	–	–	+	–	+	+	–
<i>Lambornella trichoglossa</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Leptopharynx bromelicola</i>	–	–	–	+	–	–	–	–	–	+	–
<i>Leptopharynx bromeliophilus</i>	+	+	+	+	–	–	–	+	+	+	–
<i>Leptopharynx costatus</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Mykophagophrys terricola</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Odontochlamys gouraudi</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Opercularia</i> sp.	+	–	–	–	–	–	–	–	–	–	–
<i>Oxytricha opisthomuscorum</i>	–	–	+	–	–	–	–	–	–	–	–
<i>Oxytricha setigera</i>	–	–	–	–	+	–	–	–	–	–	–
<i>Oxytricha</i> (undescribed sp. 1)	–	–	–	–	–	+	–	–	–	–	–
<i>Oxytricha</i> (undescribed sp. 2)	–	–	–	–	–	–	–	–	–	–	–
Peritrich 1	–	–	–	–	–	–	–	–	–	–	–
Peritrich 2	+	–	–	–	–	–	–	–	–	–	–
Peritrich 3	–	–	–	–	–	–	–	–	–	–	–
Peritrich 4	–	–	–	–	–	–	–	–	–	–	–
<i>Pharyngospathidium longichilum amphoriforme</i> ³	–	–	–	–	–	–	–	–	–	–	–
<i>Plagiocampa</i> sp.	–	–	–	–	–	–	–	–	–	–	–
<i>Platyophyra bromelicola</i>	–	–	–	–	–	–	–	–	–	–	–
<i>Podophrya</i> sp.	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudocyrtolophosis alpestris</i>	–	–	+	–	–	–	–	–	–	–	–
<i>Pseudourostyla franzi</i>	–	–	–	+	–	–	–	–	–	–	–
<i>Sathrophilus muscorum</i>	–	–	–	–	–	–	–	–	–	–	–
Spathidiida sp. 1	+	–	+	–	–	–	–	–	–	–	–
Spathidiida sp. 2	–	–	–	–	–	–	+	–	–	–	–

Table 1. (Continued)

Species ²	30	31	32	33	34	35	36	37	38
<i>Cyrtohymena quadrinucleata</i>	–	–	+	–	–	–	–	–	–
<i>Cyrtolophosis mucicola</i>	–	–	–	–	–	–	–	–	–
<i>Drepanomonas pauciciliata</i>	–	–	+	–	–	–	–	–	–
<i>Drepanomonas revoluta</i>	+	–	+	–	–	–	–	–	–
<i>Euplotes</i> sp.	–	–	–	–	–	–	–	–	–
<i>Frontonia depressa</i>	–	–	–	–	–	+	–	–	–
<i>Gastrostyla</i> (undescribed sp.)	–	–	–	–	–	–	–	–	–
<i>Glaucomides bromelicola</i>	+	–	+	–	–	–	–	–	–
<i>Gonostomum affine</i>	–	–	–	–	–	–	–	–	–
<i>Gonostomum kuehnelti</i>	–	–	–	–	–	–	–	–	–
<i>Halteria grandinella</i>	–	–	+	–	+	+	+	+	+
<i>Holosticha muscorum</i>	–	–	–	–	–	–	–	–	–
<i>Lambornella</i> (undescribed sp.)	+	+	+	+	–	–	–	–	–
<i>Lambornella trichoglossa</i>	+	–	–	–	–	–	–	–	–
<i>Leptopharynx bromelicola</i>	+	–	+	–	–	–	–	+	+
<i>Leptopharynx bromeliophilus</i>	+	–	+	+	–	–	+	–	–
<i>Leptopharynx costatus</i>	–	+	+	–	+	+	+	–	–
<i>Mykophagophrys terricola</i>	–	–	–	–	–	–	–	–	–
<i>Odontochlamys gouraudi</i>	–	–	+	–	+	–	–	+	–
<i>Opercularia</i> sp.	–	–	–	–	–	–	–	–	–
<i>Oxytricha opisthomuscorum</i>	–	–	–	–	–	–	–	–	–
<i>Oxytricha setigera</i>	–	–	–	–	–	–	–	–	–
<i>Oxytricha</i> (undescribed sp. 1)	–	–	–	–	–	–	–	–	–
<i>Oxytricha</i> (undescribed sp. 2)	–	–	–	–	+	–	–	–	–
Peritrich 1	–	–	–	–	–	–	–	–	–
Peritrich 2	+	–	–	–	–	–	–	–	–
Peritrich 3	–	–	–	–	–	–	–	–	–
Peritrich 4	+	–	–	–	–	–	–	–	–
<i>Pharyngospathidium longichilum amphoriforme</i> ³	–	–	–	–	–	–	–	–	–
<i>Plagiocampa</i> sp.	–	–	–	–	–	–	–	–	–
<i>Platyophyra bromelicola</i>	–	–	–	–	–	–	–	–	–
<i>Podophrya</i> sp.	–	–	–	–	–	–	–	–	–
<i>Pseudocyrtolophosis alpestris</i>	–	–	–	–	–	–	–	–	–
<i>Pseudourostyla franzi</i>	–	–	–	–	–	–	–	–	–
<i>Sathrophilus muscorum</i>	–	–	–	–	–	–	–	–	–
Spathidiida sp. 1	–	–	–	–	–	–	–	–	–
Spathidiida sp. 2	–	–	–	–	–	–	–	–	–
<i>Spathidium claviforme</i>	–	–	+	–	–	–	–	–	–
<i>Sterkiella cavicola</i>	–	–	–	–	–	–	–	–	–
<i>Tetrahymena rostrata</i>	–	–	–	–	–	–	–	–	–
<i>Tokophrya infusionum</i>	–	–	–	–	–	–	–	–	–
<i>Tokophrya</i> sp.	–	–	–	–	–	–	–	–	+
<i>Uroleptus lepisma</i>	–	–	–	–	–	–	–	–	–
<i>Vorticellides aquadulcis</i>	–	–	–	+	–	–	+	–	+
Bromeliad's host tree species ⁴	Co	Dt	Tm	Bs	As	Lg	Lg	Ej	Ej
Number of species in sample	10	2	15	3	4	4	4	3	5
Species ²	39	40	41	42	43	44	45	46	47
<i>Acineta</i> sp.	–	–	–	–	–	–	–	–	–
<i>Arcuospathidium namibiense tristicha</i>	–	–	–	–	–	–	–	–	–
<i>Arcuospathidium cultriforme scalpriforme</i>	–	–	–	+	–	–	–	–	–
<i>Blepharisma steini</i>	–	–	–	+	–	–	–	–	–
<i>Bromeliothrix metopoides</i>	–	–	–	–	–	–	–	–	–
<i>Chilodonella uncinata</i>	–	–	+	+	+	+	–	–	–
<i>Colpoda cucullus</i>	–	–	–	–	+	–	–	–	–

Table 1. (Continued)

Species ²	39	40	41	42	43	44	45	46	47
<i>Colpoda henneguyi</i>	–	–	+	–	–	–	–	–	–
<i>Colpoda inflata</i>	–	–	+	–	–	–	–	–	–
<i>Colpoda lucida</i>	–	–	–	+	+	+	–	–	–
<i>Colpoda maupasi</i>	–	–	–	+	+	–	–	–	–
<i>Colpoda steinii</i>	–	–	–	–	–	–	–	–	–
<i>Coriplites proctori</i>	–	–	+	+	–	+	–	–	–
<i>Cotterillia bromelicola</i>	–	–	–	+	–	–	–	–	–
<i>Ctedoctema</i> sp.	–	–	–	–	–	–	–	–	–
<i>Cyclidium glaucoma</i>	–	–	–	–	+	–	–	–	–
<i>Cyclidium muscicola</i>	–	–	–	+	–	–	–	–	–
<i>Cyrtohymena quadrinucleata</i>	–	–	+	+	+	+	+	–	–
<i>Cyrtolophosis mucicola</i>	–	–	–	–	–	+	–	–	–
<i>Drepanomonas pauciciliata</i>	–	–	–	–	+	–	–	–	–
<i>Drepanomonas revoluta</i>	–	+	–	–	+	–	+	–	–
<i>Euplotes</i> sp.	–	–	–	+	–	–	–	–	–
<i>Frontonia depressa</i>	–	–	–	+	–	–	+	–	–
<i>Gastrostyla</i> (undescr. sp.)	–	–	–	–	–	+	–	–	–
<i>Glaucoides bromelicola</i>	+	–	+	+	+	–	–	–	+
<i>Gonostomum affine</i>	–	–	–	–	–	–	–	–	–
<i>Gonostomum kuehnelti</i>	–	–	–	–	–	+	–	–	–
<i>Halteria grandinella</i>	–	+	–	–	+	–	+	+	–
<i>Holosticha muscorum</i>	–	–	–	–	–	–	–	–	–
<i>Lambornella</i> (undescr. sp.)	+	–	–	–	–	–	–	–	+
<i>Lambornella trichoglossa</i>	–	–	–	–	–	–	–	–	–
<i>Leptopharynx bromelicola</i>	+	–	–	+	+	+	+	+	–
<i>Leptopharynx bromeliophilus</i>	–	–	–	–	+	–	+	–	+
<i>Leptopharynx costatus</i>	–	–	+	+	+	+	–	–	–
<i>Mykophagophrys terricola</i>	–	–	–	–	–	–	–	–	–
<i>Odontochlamys gouraudi</i>	–	–	+	–	–	–	–	–	–
<i>Opercularia</i> sp.	–	–	–	–	–	–	–	–	–
<i>Oxytricha opisthomuscorum</i>	–	–	–	–	–	–	–	–	–
<i>Oxytricha setigera</i>	–	–	–	+	–	–	–	–	–
<i>Oxytricha</i> (undescr. sp. 1)	–	–	–	–	–	+	–	–	–
<i>Oxytricha</i> (undescr. sp. 2)	–	–	–	–	–	+	–	–	–
Peritrich 1	–	–	–	–	–	–	+	–	–
Peritrich 2	–	–	–	–	–	–	–	–	–
Peritrich 3	–	–	–	–	+	–	–	–	–
Peritrich 4	–	–	–	–	–	–	–	–	–
<i>Pharyngospathidium longichilum amphoriforme</i> ³	–	–	–	–	–	–	+	–	–
<i>Plagiocampa</i> sp.	–	–	–	–	–	–	–	–	–
<i>Platyophya bromelicola</i>	–	–	–	–	–	–	–	–	–
<i>Podophrya</i> sp.	–	–	–	–	–	–	–	–	–
<i>Pseudocyrtolophosis alpestris</i>	–	–	–	–	–	–	–	–	–
<i>Pseudourostyla franzi</i>	–	–	–	–	–	+	–	–	–
<i>Sathrophilus muscorum</i>	–	–	–	–	+	–	–	–	–
Spathidiida sp. 1	–	–	–	+	–	–	–	–	–
Spathidiida sp. 2	–	–	–	–	–	–	+	–	–
<i>Spathidium claviforme</i>	–	–	–	–	–	–	–	–	–
<i>Sterkiella cavicola</i>	–	–	–	–	+	–	–	–	–
<i>Tetrahymena rostrata</i>	–	–	–	–	–	–	–	–	–
<i>Tokophrya infusioformis</i>	–	–	–	–	–	–	–	–	–
<i>Tokophrya</i> sp.	–	–	–	–	–	–	–	–	–
<i>Uroleptus lepisma</i>	–	–	–	–	–	–	–	–	–
<i>Vorticellides aquadulcis</i>	–	+	–	+	–	–	+	–	–
Bromeliad's host tree species ⁴	Ej	Ej	Ln	Fr	Lg	Lg	Fc	Fc	Iv
Number of species in sample	3	3	8	17	16	12	10	2	3

Table 1. (Continued)

Species ²	48	49	50	51	52	Records
<i>Acineta</i> sp.	–	–	–	–	–	1
<i>Arcuospathidium namibiense tristicha</i>	–	–	–	–	–	3
<i>Arcuospathidium cultriforme scalpriforme</i>	–	–	–	–	–	2
<i>Blepharisma steini</i>	–	–	–	–	–	2
<i>Bromeliothrix metopoides</i>	–	–	–	+	+	4
<i>Chilodonella uncinata</i>	+	–	–	–	–	15
<i>Colpoda cucullus</i>	–	–	–	–	–	6
<i>Colpoda henneguyi</i>	+	–	+	–	–	8
<i>Colpoda inflata</i>	–	–	–	–	–	3
<i>Colpoda lucida</i>	–	–	–	–	–	18
<i>Colpoda maupasi</i>	–	–	–	–	–	6
<i>Colpoda steinii</i>	–	–	–	–	–	7
<i>Coriplites proctori</i>	–	–	+	+	–	8
<i>Cotterillia bromelicola</i>	+	–	–	–	–	5
<i>Ctedoctema</i> sp.	–	–	–	–	–	1
<i>Cyclidium glaucoma</i>	–	–	–	–	–	20
<i>Cyclidium muscicola</i>	–	–	–	–	–	4
<i>Cyrtohymena quadrinucleata</i>	–	–	–	–	–	7
<i>Cyrtolophosis mucicola</i>	–	–	–	–	–	3
<i>Drepanomonas pauciciliata</i>	–	–	–	–	–	5
<i>Drepanomonas revoluta</i>	–	–	–	–	–	10
<i>Euplotes</i> sp.	–	–	–	–	+	2
<i>Frontonia depressa</i>	–	–	–	–	–	8
<i>Gastrostyla</i> (undescr. sp.)	–	–	–	–	–	4
<i>Glaucoides bromelicola</i>	–	–	–	–	–	19
<i>Gonostomum affine</i>	–	–	–	–	–	1
<i>Gonostomum kuehnelti</i>	–	–	–	–	–	1
<i>Halteria grandinella</i>	–	–	–	–	–	22
<i>Holosticha muscorum</i>	–	–	–	–	–	4
<i>Lambornella</i> (undescr. sp.)	–	–	–	+	+	24
<i>Lambornella trichoglossa</i>	–	–	–	–	+	2
<i>Leptopharynx bromelicola</i>	+	+	+	+	–	22
<i>Leptopharynx bromeliophilus</i>	+	+	+	+	–	25
<i>Leptopharynx costatus</i>	+	+	+	+	–	18
<i>Mykophagophrys terricola</i>	–	–	–	–	–	1
<i>Odontochlamys gouraudi</i>	–	–	–	–	–	4
<i>Opercularia</i> sp.	–	–	–	–	–	3
<i>Oxytricha opisthomuscorum</i>	–	–	–	–	–	1
<i>Oxytricha setigera</i>	–	–	–	–	–	3
<i>Oxytricha</i> (undescr. sp. 1)	–	–	–	–	–	4
<i>Oxytricha</i> (undescr. sp. 2)	–	–	–	–	–	4
Peritrich 1	–	–	–	–	–	1
Peritrich 2	–	–	–	–	–	2
Peritrich 3	–	–	–	–	–	1
Peritrich 4	–	–	–	–	–	1
<i>Pharyngospathidium longichilum amphoriforme</i> ³	–	–	–	–	–	3
<i>Plagiocampa</i> sp.	–	–	–	–	–	1
<i>Platyophyra bromelicola</i>	–	–	–	–	–	2
<i>Podophrya</i> sp.	–	–	–	–	–	1
<i>Pseudocyrtolophosis alpestris</i>	–	–	–	+	–	4
<i>Pseudourostyla franzi</i>	–	–	–	–	–	2
<i>Sathrophilus muscorum</i>	–	–	–	–	–	1
Spathidiida sp. 1	–	–	–	–	–	3
Spathidiida sp. 2	–	–	–	–	–	3

Table 1. (Continued)

Species ²	48	49	50	51	52	Records
<i>Spathidium claviforme</i>	–	–	–	–	–	1
<i>Sterkiella cavicola</i>	–	–	–	–	–	1
<i>Tetrahymena rostrata</i>	–	–	–	–	–	1
<i>Tokophrya infusioenum</i>	–	–	–	–	–	2
<i>Tokophrya</i> sp.	–	–	–	–	–	1
<i>Uroleptus lepisma</i>	–	–	–	–	–	3
<i>Vorticellides aquadulcis</i>	+	–	–	–	–	17
Bromeliad's host tree species ⁴	Ln	Qc	Qc	Qc	Qc	
Number of species in sample	7	3	5	7	4	

¹ Samples 1–16, area 1; 17–32, area 2; 33–48, area 3, 49–52, area 4. For description of sites, see material and methods. +, present; –, absent.

² Species authorship are according to Berger (1999, 2006); Foissner (1993, 1998); Foissner and Xu (2007); Foissner et al. (2002), and species description papers.

³ Description in preparation.

⁴ Bromeliad's host tree species. **As**, *Acacia* sp.; **Bd**, *Bauhinia* aff. *divaricata*; **Bs**, *Bursera* aff. *simaruba*; **Co**, *Cecropia obtusifolia*; **Cl**, *Citrus limon*; **Cb**, *Cupressus benthami* var. *lindleyi*; **Da**, *Dendropanax arboreus*; **Ej**, *Eugenia jambos*; **Es**, *Eugenia* sp.; **Fc**, *Ficus cotinifolia*; **Fr**, *Ficus crocata*; **Iv**, *Inga vera*; **Ln**, Leguminosae; **Lg**, *Lonchocarpus guatemalensis*; **Ma**, *Meliosma alba*; **Mi**, Mimosaceae; **Ns**, *Nectandra* sp.; **Qc**, *Quercus castanea*; **Qx**, *Quercus* aff. *xalapensis*; **Rm**, *Rapanea myricoides*; **Sp**, *Spondias purpurea*; **Tm**, *Trema micrantha*; **Dt**, Death tree.

ciliate species (5.07 ± 2.82) while nine samples (17.3%) contained 12–18 species (14.8 ± 2.04) (Table 1).

A total of 61 ciliate species belonging to 39 genera were observed during the survey. Ten species were present in both *T. heterophylla* and *T. prodigiosa*. The species recorded were grouped in eight classes according to the system proposed by Lynn (2008). More than two-thirds of the isolates belong to three classes: Spirotrichea (16), Oligohymenophorea (14) and Colpodea (12) (Table 2).

Based on the review of Aladro-Lubel et al. (2006) more than 50% (33 out of 61) of the ciliate species isolated in the present study are recorded for the first time in Mexico and almost 40% (24 out of 61) are recorded for the first time in bromeliads (Table 2). *Colpoda* was the genus with the highest number of species (6). The undescribed species of the genera *Gastrostyla*, *Lambornella* and *Oxytricha* (Table 1) seem to be the same reported by Dunthorn et al. (2012).

Of the 61 recorded species, 51 (83.6%) were rare since they were present in no more than 10 of the 52 samples analyzed (3.16 ± 2.28) (Table 1). Sixteen of these species, each present in only one sample, count for 26.2% of the total, namely *Acineta* sp., *Ctedoctema* sp., *Gonostomum affine*, *Gonostomum kuehnelti*, *Mykophagophrys terricola*, *Oxytricha opisthomuscorum*, peritrichs 1, 3 and 4, *Plagiocampa* sp., *Podophrya* sp., *Sathrophilus muscorum*, *Spathidium claviforme*, *Sterkiella cavicola*, *Tetrahymena rostrata* and *Tokophrya* sp. Furthermore, they also tended to have low individual abundances and were therefore thought to be casual colonizers. By contrast, ten species were recorded in 15–25 samples (20 ± 3.2), namely *Chilodonella uncinata*, *Colpoda lucida*, *Cyclidium glaucoma*, *Glaucomides bromelicola*, *Halteria grandinella*, *Lambornella* (undescribed species), *Leptopharynx bromelicola*, *Leptopharynx bromeliophilus*, *Leptopharynx costatus* and *Vorticellides aquadulcis*,

represent 16.4% of the total (Table 1). *L. bromeliophilus* was the most frequent species being present in 25 samples.

Samples 1, 4, 20, 27, 32, 42 and 43 from *T. heterophylla* presented the highest number of species (between 14 and 18); most of them were collected at coffee plantations (areas 2 and 3), just with the exception of two (samples 1, 4). Within this group of seven samples we found that 9–12 species are considered as soil inhabitants (Foissner 1998) and 3–6 have been previously recorded only in bromeliads (Dunthorn et al. 2012). In the same group of samples, we also observed from 1–5 species of genus *Colpoda* that were always present, as well as *L. bromelicola* and *L. bromeliophilus*. In contrast, 12 samples collected from areas 1, 2 and 3 from *T. heterophylla*, showed the lowest number of species (0–5), with the presence of one or two species endemic to bromeliads, i.e. *G. bromelicola*, in almost all the samples (Table 1). Samples 35 and 36, obtained from two adjacent individuals of *T. heterophylla* shared *H. grandinella* and *L. costatus*, and showed the same number of species (Table 1). In area 4, we recorded 3–7 species, including *L. bromelicola*, *L. bromeliophilus* and *L. costatus*, from the four samples obtained from *T. prodigiosa*, where *Quercus castanea* was the only host tree (Figs 2–12).

Only in the case of *T. heterophylla*, we observed that it is possible that some ciliate species show different abundances within the tank when they were collected. *Colpoda maupasii*, *H. grandinella*, *Lambornella* (undescribed species) and *L. bromelicola* showed the higher abundances in samples collected from areas 1, 2 and 3 (unpubl.). Also we observed a different number of species in each plant, even in those growing close together. Through an application of Jaccard index we assessed the similarity at the community level. A low similarity between areas and seasons was observed from 0.10 to 0.52 (0.32 ± 0.11) (Fig. 13). The shared species between areas and seasons were from 4 to 24 (13.3 ± 6.5).

Table 2. (Continued)

Species	Class ²	Country ¹								
		B	CH	CR	E	J	M	P	RD	V
<i>Spathidiida</i> sp. 1	LI	–	–	–	–	–	–	–	–	–
<i>Spathidiida</i> sp. 2	LI	–	–	–	–	–	–	–	–	–
<i>Spathidium claviforme</i>	LI	–	–	–	–	–	–	–	–	–
<i>Sterkiella cavicola</i>	SP	–	–	–	–	–	–	–	–	–
<i>Tetrahymena rostrata</i>	OL	+	–	–	–	–	–	–	+	–
<i>Tokophrya infusionum</i>	PH	–	–	–	–	–	+	–	+	–
<i>Tokophrya</i> sp.	PH	–	–	–	–	–	–	–	–	–
<i>Uroleptus lepisma</i>	SP	–	–	–	+	–	–	–	+	–
<i>Vorticellides aquadulcis</i>	OL	+	–	–	–	–	+	–	–	–
Species		Reference ³			NM			NB		
<i>Acineta</i> sp.		TS			–			+		
<i>Arcuospathidium namibiense tristicha</i>		TS			+			+		
<i>Arcuospathidium cultriforme scalpriforme</i>		TS			+			+		
<i>Blepharisma steini</i>		TS			–			+		
<i>Bromeliothrix metopoides</i>		3			+			–		
<i>Chilodonella uncinata</i>		7			–			–		
<i>Colpoda cucullus</i>		7			–			–		
<i>Colpoda henneguyi</i>		TS			+			+		
<i>Colpoda inflata</i>		7			–			–		
<i>Colpoda lucida</i>		7			+			–		
<i>Colpoda maupasi</i>		7			–			–		
<i>Colpoda steinii</i>		7			–			–		
<i>Coriplites proctori</i>		9			+			–		
<i>Cotterillia bromelicola</i>		6, 1			+			–		
<i>Ctedoctema</i> sp.		TS			–			+		
<i>Cyclidium glaucoma</i>		7			–			–		
<i>Cyclidium muscicola</i>		7			+			–		
<i>Cyrtohymena quadrinucleata</i>		TS			+			+		
<i>Cyrtolophosis mucicola</i>		7			+			–		
<i>Drepanomonas pauciciliata</i>		TS			+			+		
<i>Drepanomonas revoluta</i>		7			+			–		
<i>Euplotes</i> sp.		TS			–			+		
<i>Frontonia depressa</i>		7			+			–		
<i>Gastrostyla</i> (undescribed sp.)		1			–			–		
<i>Glaucoides bromelicola</i>		4			+			–		
<i>Gonostomum affine</i>		TS			+			+		
<i>Gonostomum kuehnelti</i>		TS			+			+		
<i>Halteria grandinella</i>		7			–			–		
<i>Holosticha muscorum</i>		TS			+			+		
<i>Lambornella</i>		1			–			–		
<i>Lambornella trichoglossa</i>		2, 7			+			–		
<i>Leptopharynx bromelicola</i>		8			+			–		
<i>Leptopharynx bromeliophilus</i>		10			+			–		
<i>Leptopharynx costatus</i>		7, 8			+			–		
<i>Mykophagophrys terricola</i>		TS			+			+		
<i>Odontochlamys gouraudi</i>		TS			+			+		
<i>Opercularia</i> sp.		TS			–			+		
<i>Oxytricha opisthomuscorum</i>		TS			+			+		
<i>Oxytricha setigera</i>		TS			+			+		
<i>Oxytricha</i> (undescribed sp. 1)		1			–			–		
<i>Oxytricha</i> (undescribed sp. 2)		1			–			–		
<i>Peritrich</i> sp. 1		TS			–			–		
<i>Peritrich</i> sp. 2		TS			–			–		
<i>Peritrich</i> sp. 3		TS			–			–		

Table 2. (Continued)

Species	Reference ³	NM	NB
Peritrich sp. 4	TS	–	–
<i>Pharyngospathidium longichilum amphoriforme</i>	TS	+	+
<i>Plagiocampa</i> sp.	TS	–	+
<i>Platyophrya bromelicola</i>	5	+	–
<i>Podophrya</i> sp.	TS	–	+
<i>Pseudocyrtilophosis alpestris</i>	7	+	–
<i>Pseudourostyla franzi</i>	TS	+	+
<i>Sathrophilus muscorum</i>	7	–	–
Spathidiida sp. 1	TS	–	–
Spathidiida sp. 2	TS	–	–
<i>Spathidium claviforme</i>	TS	+	+
<i>Sterkiella cavicola</i>	TS	+	+
<i>Tetrahymena rostrata</i>	7	+	–
<i>Tokophrya infusionum</i>	1	–	–
<i>Tokophrya</i> sp.	TS	–	+
<i>Uroleptus lepisma</i>	7	+	–
<i>Vorticellides aquadulcis</i>	7	–	–

¹ Abbreviation of countries: **B**, Brazil; **CH**, Chile; **CR**, Costa Rica; **E**, Ecuador; **J**, Jamaica; **M**, Mexico; **P**, Peru; **DR**, Dominican Republic; **V**, Venezuela; **TS**, This study. Other abbreviations: **NM**, New record for Mexico according to Aladro-Lubel et al. 2006; **NB**, First record for bromeliads. +, present; –, not recorded.

² Classes according to Lynn (2008): **CO**-Colpodea Small and Lynn, 1981; **HE**-Heterotrichea Stein, 1859; **LI**-Litostomatea Small and Lynn, 1981; **NA**-Nassophorea Small and Lynn, 1981; **OL**-Oligohymenophorea de Puytorac et al. 1974; **PH**-Phyllopharyngea de Puytorac et al. 1974; **PR**-Prostomatea Schewiakoff, 1896; **SP**-Spirotrichea Bütschli, 1889.

³ References: 1. Dunthorn et al. (2012); 2. Foissner (2003b); 3. Foissner (2010); 4. Foissner (2013); 5. Foissner and Stoeck (2011); 6. Foissner and Wolf (2009); 7. Foissner et al. (2003); 8. Foissner et al. (2011); 9. Oertel et al. (2009); 10. Omar and Foissner (2011).

Area 2 during the dry season and area 3 during the humid season showed the highest similarity (0.52). Area 4 showed the lowest similarity to areas 1, 2 and 3.

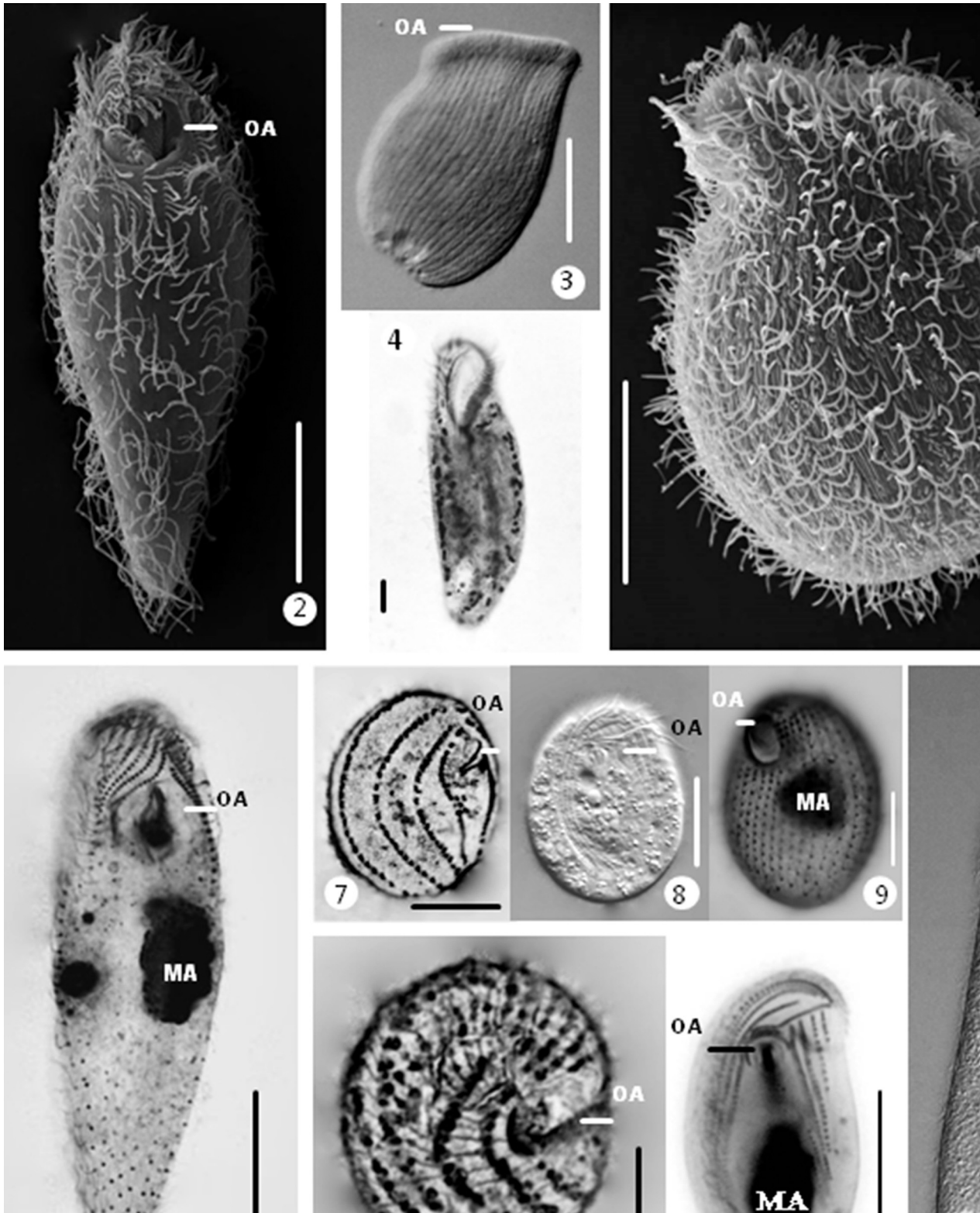
Discussion

The number of species recorded from the two bromeliad species investigated in Mexico was 61. Until 2012, only eleven ciliate species inhabiting bromeliads have been reported from Mexico (Dunthorn et al. 2012; Foissner 2010; Foissner and Stoeck 2011; Foissner et al. 2011; Omar and Foissner 2011). The taxonomic list of the present study includes 50 additional records and all together represent the longest list of ciliate species from tank bromeliads.

We found a large number (28) of cosmopolitan euryoecious ciliate species such as *C. glaucoma*, *C. uncinata* and *Colpoda cucullus*, occurring in soil, freshwater and bromeliads (Foissner, 1995, 1997, 1998, 1999; Foissner et al. 2002). *Colpoda inflata*, *C. maupasi*, *C. steinii*, *Cyrtolophosis mucicola*, *Drepanomonas* spp., *G. affine*, *Leptopharynx* spp. and *Pseudocyrtilophosis alpestris* are common species in soils of tropical forests and in moss (Foissner 1997, 1998). One of the peculiarities of the ciliates that inhabit soils and bromeliads is their ability to form resistant cysts, which allows them to survive adverse conditions, specifically short droughts and too strong competition for food (Foissner 1987).

The prevalence of colpodids (class Colpodea) and hypotrichs (class Spirotrichea) is common in soil ciliate communities (Foissner 1987). In *T. heterophylla*, the class Spirotrichea and the genus *Colpoda* showed the highest diversity with 13 and 6 taxa, respectively (Table 1). The colpodids are considered as one of the main groups of bacterivores in terrestrial and semiterrestrial environments. The smaller species of *Colpoda* usually ingest bacteria or other particulate food of similar size, whereas some larger species feed on unicellular algae, filamentous cyanobacteria, other protozoans, and occasionally rotifers or other microzooplankton (Finlay and Esteban 1998; Foissner, 1993). In this way, the morphological adaptations allow certain species to live in soil (Foissner, 1987) and possibly also in bromeliads.

On the other hand, species like *Bromeliothrix metopoides*, *C. bromelicola*, *Gastrostyla* (undescribed sp.), *G. bromelicola*, *Lambornella trichoglossa*, *L. bromelicola*, *Oxytricha* (undescribed sp. 1) and *Platyophrya bromelicola* are considered as endemic to phytotelmata, specially in the bromeliad environment (Dunthorn et al. 2012; Foissner, 2003b). Furthermore, there are no records of these species from other environments of Mexico. These observations confirm their specificity to these microecosystems in the Neotropics. According to Dunthorn et al. (2012), there is no evidence of specificity for certain bromeliad species. However, the specificity at microecosystem level of certain ciliate species is probably due to the alternating presence and absence of water, their spatial isolation, and the competition for resources (Foissner, 2005).



Figs. 2–12. Ciliates from the tanks of *Tillandsia heterophylla* in the scanning electron microscope (2, 5), in vivo (3, 8, 12), after protargol (4, 6, 9, 11) and silver nitrate impregnation (7, 10). 2, 6. *Lambornella* sp. 3, 5. *Pharyngospathidium longichilum amphoriforme* (unpubl. sp.). 4. *Pseudourostyla franzi*. 7. *Leptopharynx bromelicola*. 8. *Odontochlamys gouraudi*. 9. *Glaucomides bromelicola*. 10. *Bromeliothrix metopoides*. 11. *Chilodonella uncinata*. 12. *Arcuospathidium cultriforme scalpriforme*. MA: macronucleus. OA: oral apparatus. Scale bar 20 μm .

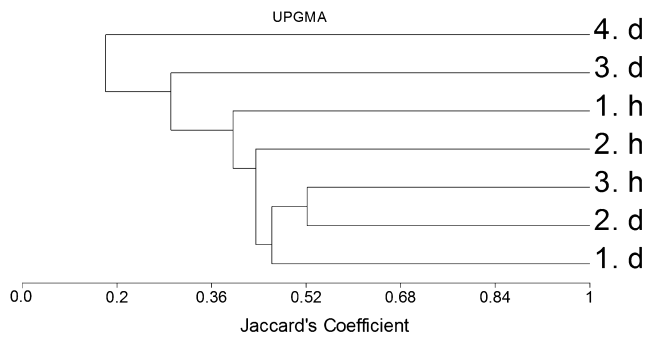


Fig. 13. Dendrogram that shows similarity between areas and seasons with Jaccard index. Numbers represent sites; d, dry season, h, humid season.

Number of motile ciliates species was higher than sessile ones. Some peritrichs from bromeliads were recently described (Foissner et al. 2009). The peritrichs (class Oligohymenophorea), a group of bacterivorous filter-feeders that usually attach to a substrate, were represented by six species, but four of them could not be identified. Other sessile ciliates isolated in the present study included three genera of suctorians (class Phyllopharyngea) three of which, namely *Acineta* sp., *Podophrya* sp. and *Tokophrya* sp. are probably undescribed (I. Dovgal, pers. com.). However, their low abundance, as in peritrich species 1–4, prevented their detailed characterization. *Tokophrya infusionum* is the only suctorian species that has been previously recorded in a sample of *T. heterophylla* from Mexico (Dunthorn et al. 2012). It is noteworthy that this is the first record of suctorians in bromeliads in the Neotropics. The relative scarcity of sessile ciliates is probably a result of the method used for collecting the samples, which excluded substrates such as Metazoa that offer potential attachment sites.

Like suctorians, most haptorids are carnivorous and their presence in bromeliads is rather unusual (Foissner et al. 2003); however, six species of haptorids were isolated in the present study, all being predators of other ciliate species (Table 1).

The geographical distribution of certain species, such as *L. trichoglossa* (Foissner, 2003b) is now extended. *L. trichoglossa* was described in bromeliads from Brazil, Ecuador and the Dominican Republic but, despite its remarkable size, it has not been observed in other regions of the world. For this reason, Foissner (2003b) considered it a Gondwanian species with a distribution restricted to South America. The presence of this species in Mexican samples from a temperate mountain forest located almost 2000 m above sea level suggests that it tolerates wide temperature ranges and has a broader distribution.

Foissner et al. (2003) and Dunthorn et al. (2012) established that the ciliate fauna of bromeliads differs from that of other limnetic habitats. Genera such as *Frontonia*, *Paramecium* and *Glaucoma* are common in freshwater environments, but were considered to be absent in bromeliads. However,

Buosi et al. (2014) recorded *Paramecium multimicronucleatum* from bromeliads located close to a river from the south of Brazil, and in the present study, we recorded *Frontonia depressa*, which is a common species in moss and soil.

The genus *Leptopharynx*, which is not very common in limnetic environments (Omar and Foissner 2011), is represented by three species in Mexican bromeliads, two of which were previously recorded in bromeliads from Jamaica (Foissner et al. 2011; Omar and Foissner 2011) while *L. costatus* was recorded in bromeliads from the Dominican Republic, Costa Rica, Ecuador and Peru (Table 2). Omar and Foissner (2011) mentioned that *L. bromeliophilus* could be confused with *L. costatus* but the former has a smaller size and does not have a microstome form.

B. metopoides has a wide continental distribution but is thought to be restricted to bromeliads since it has not been recorded in any of more than thousand soil samples collected globally (Foissner 2008, 2010). Foissner (2010) considered this ciliate as a flagship species because of its peculiar division process during which it forms chains of four individuals. Another remarkable species was *Cotterillia bromelicola* which has been previously recorded inhabiting *T. heterophylla* (Foissner and Stoeck 2011). It has not been detected in other bromeliad species or in soil samples (Foissner 1998; Foissner et al. 2002) and its specificity in tank bromeliads is not known. Moreover, Sigala-Regalado (pers. com.) observed *C. bromelicola* in moss samples at the entrance of a cave surrounded by mountain cloud forest close to its type locality. This finding suggests that *C. bromelicola* is not restricted to bromeliads and may therefore have a wider distribution than is currently recognized. On the other hand, its presence at this area could be explained by the presence of bromeliads as part of the vegetation surrounding the cave. The same has been observed in Costa Rica (W. Foissner unpubl.). It is possible that this species presents a geographical distribution restricted to this portion of the continent, either in soil, moss or bromeliads.

The taxa richness of ciliates inhabiting bromeliads from Mexico was lower in comparison to some environments, such as Neotropical flood plains (Foissner 2005), but was three times higher than that reported by Foissner et al. (2003) in bromeliads from the Dominican Republic, Ecuador (24 species) and Brazil (19 species). In addition to sharing species with bromeliads of these three countries, other ciliates isolated in the present study have previously been recorded in other five countries like Chile (Foissner, 2013), Costa Rica (Foissner et al. 2011), Jamaica (Dunthorn et al. 2012; Foissner 2013; Foissner et al. 2011; Foissner and Wolf 2009; Oertel et al. 2009; Omar and Foissner 2011), Peru (Foissner, 2013; Foissner et al. 2011) and Venezuela (Foissner, 2013) (Table 2).

The low similarity at the community level in the four areas can be explained in different ways; for example in area 4 this can be due to the 400 km of distance that separates this area from areas 1, 2 and 3 which are closer between them. Areas 1–3 have mountain cloud forest remnants with some

crops and they are located near urban areas, in contrast area 4 is a secondary forest in a slope with pine–oak trees with a lower degree of perturbation; however, its species richness was noticeably lower in comparison with areas 1–3. This indicates that seasonality and area differences do not explain the species distribution based on presence-absence data. It is probable that the degree of conservation of forest where bromeliads grow may play an important role in the assemblage of ciliate species that inhabit bromeliads, but it is not possible to establish that for area 4 due to the low sample size. We establish that there was no evident similarity at community level between areas and seasons during the present study and the species from areas 1–4 presented a random distribution pattern at spatial and temporal scale.

In the case of epiphytic bromeliads, it is not clear how the host tree species affects the ciliate community. Based on the data of species richness by sample, we can suggest that this richness could be affected by the plant position and characteristics of the canopy. In the present study, samples were collected from bromeliads attached to a total of 22 host tree species (Table 1). Chemical analyses were not carried out but we observed that the largest number of ciliate species per sample was recorded in bromeliads hosted by *Citrus limon*, *Trema micrantha*, *Ficus crocata* and *Lonchocarpus guatemalensis*. By contrast, only one individual of *T. heterophylla*, hosted by *Quercus xalapensis*, did not yield any ciliate species (sample 16, area 1). It is possible that the ciliate communities might be affected by the chemical characteristics of the leaves that accumulate and decompose in the bromeliad tank. On the other hand, samples were collected from bromeliads growing in a wide range of habitats, i.e. a mountain cloud forest, a temperate pine–oak forest and two distinctly different agroecosystems. Consequently, the ciliate communities observed are also likely to have been influenced by the environmental variation among these ecosystems, i. e. water volume, pH, and temperature.

The interactions and ecological aspects between species found in tank bromeliads are still almost unknown. Weisse et al. (2013) reported that *Glaucomides bromelicola* could coexist with *B. metopoides* because their feeding and dispersion strategies are different. We found these two species only in sample 32 associated to *Lambornella* (undescribed sp.), *L. bromelicola* and *L. bromeliophilus*, which are considered as endemic species in bromeliads (Dunthorn et al. 2012).

The removal of epiphytic plants is an agroforestry practice in the Neotropic to increase light availability for the coffee crops (Cruz-Angón and Greenberg 2005). This produces a simplification of the agroecosystem because it eliminates a key component of the plant diversity with the associated microbiota. The effect on the ciliate communities where agriculture is practiced, such as at areas 2 and 3, is also unknown. These communities can potentially be used for environmental monitoring because ciliates are well known as useful bioindicators of natural and anthropogenic environmental change (Foissner 1987; Foissner et al. 1994). Consequently, it has been suggested that ciliates should be considered within the

conservation strategies, especially in the Neotropic (Cotterill et al. 2008).

The bromeliads that host these Neotropic-exclusive ciliate communities constitute centers of important biological activity. Current knowledge is insufficient to determine the specificity of the relationship between ciliates and bromeliads. Their presence will depend mainly on bromeliad and forest conservation. Major research is required on their diversity, colonization, interaction, ecology and evolution. More sampling of different bromeliad species from different regions in the country and in the Neotropics is desirable.

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