

## 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

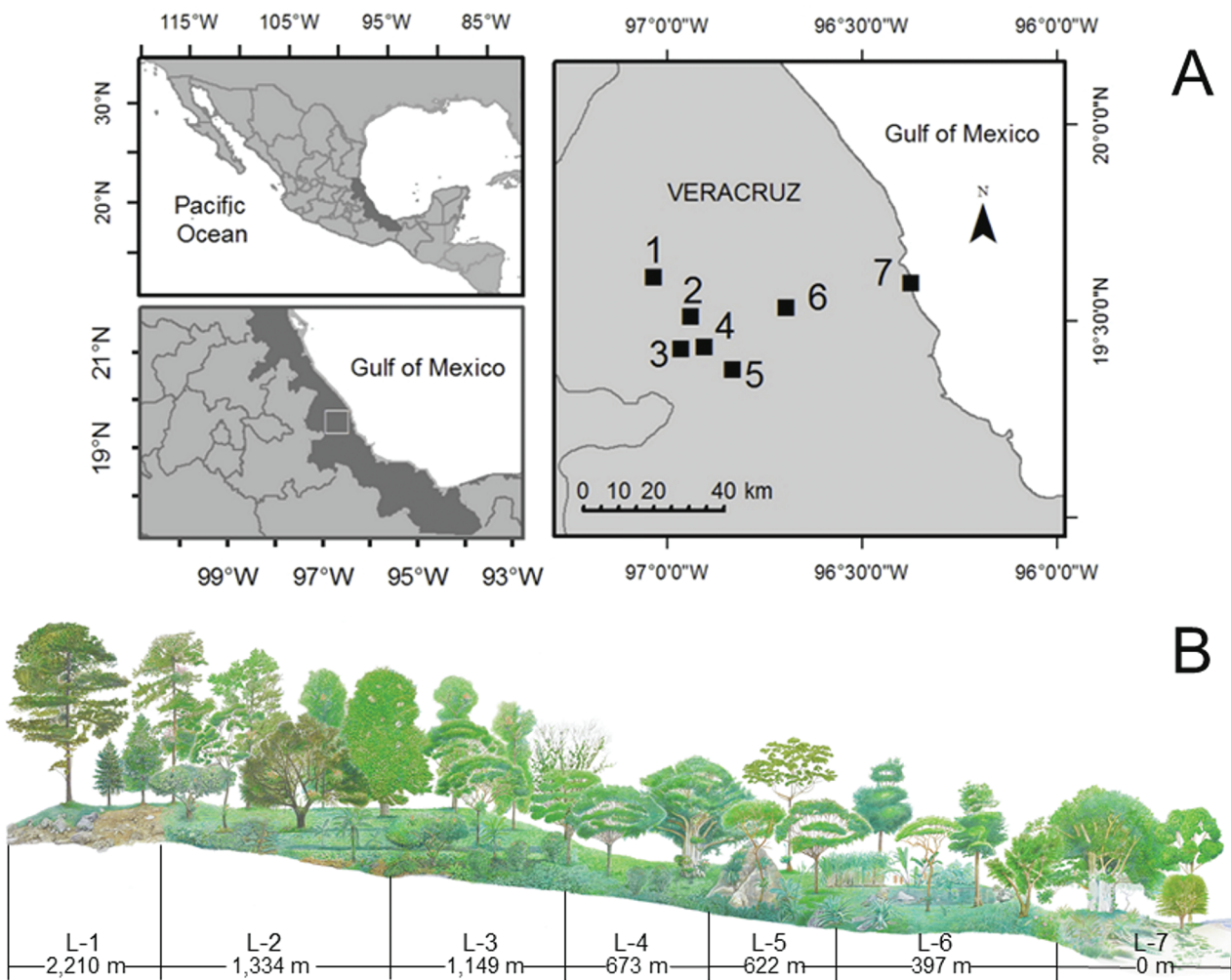
**Area of study.** We collected samples during December 2014, April and May of 2015 from seven localities in the state of Veracruz, eastern Mexico (Fig. 1), including a fragment of semideciduous tropical forest on coastal dunes along the coastal shore with only one locality; two localities with remnants 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 megapixel 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), Borrór 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 ( $J_{A,B} = c/[a+b-c]$ ), 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.

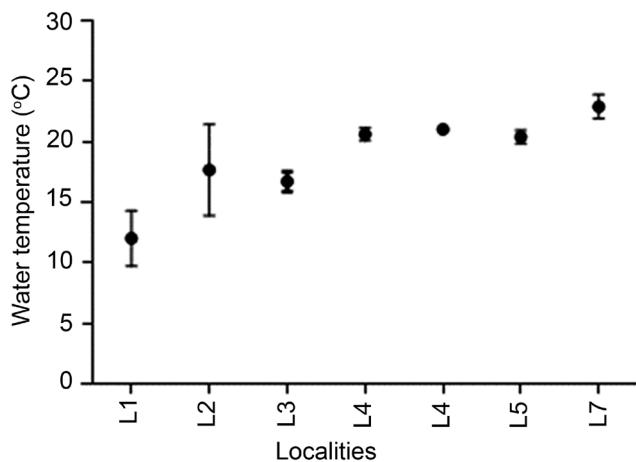
**Table 2.** Records based on presence – absence of ciliate species from bromeliads in the localities.

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 1</i>		+						
<i>Peritrichia 2</i>							+	
<i>Peritrichia telotroch</i>								+
<i>Tetrahymena</i> spp.			+	+		+		
<i>Vorticella</i> sp.								+
Total of species per locality		9	15	12	4	5	7	11

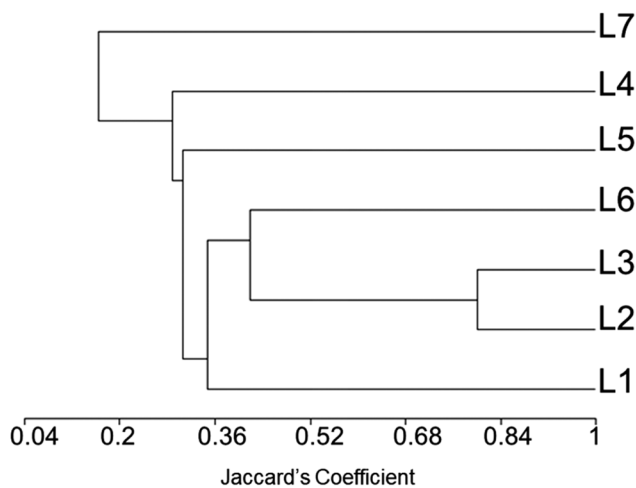
\*New record in Mexico.

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 where 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.

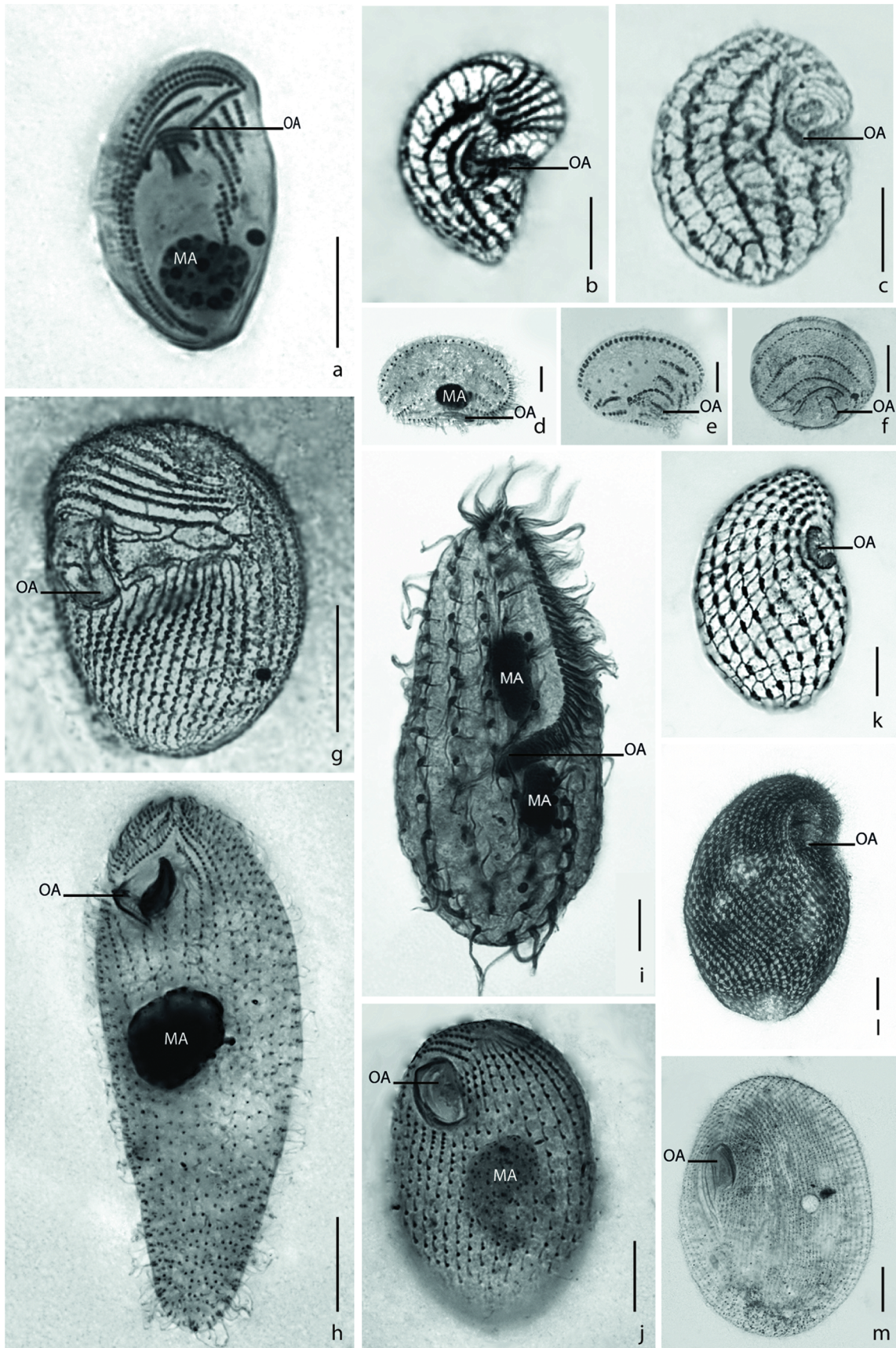
**Ciliate community structure according to localities.** Ciliate community structure was different between localities. We found that locality 2 showed

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 *Glaucomidia 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).

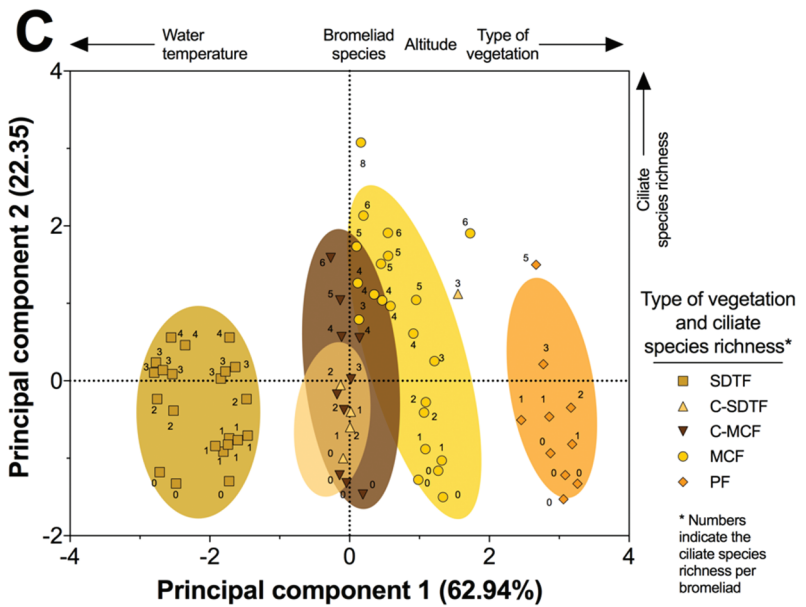
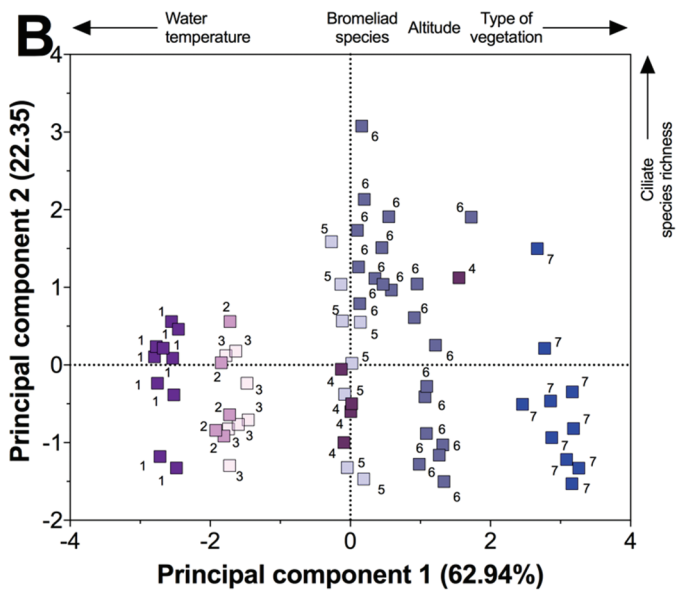
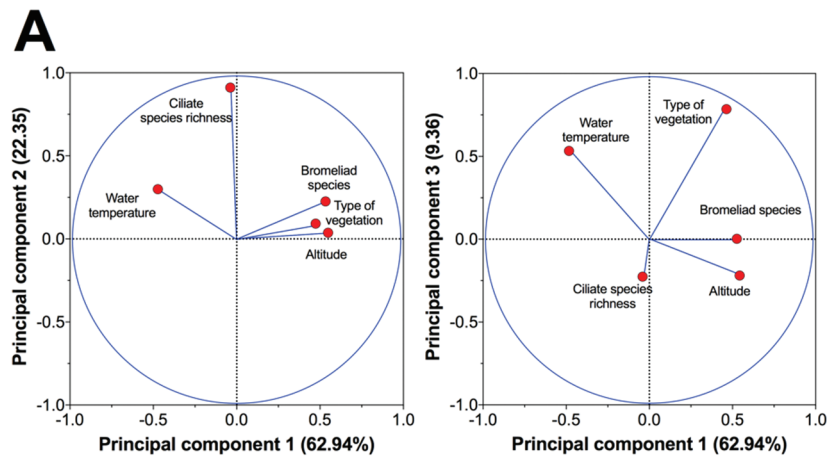
The PCA evaluated the association between ciliate community structure related to biotic (bromeliad species and type of vegetation) and abiotic factors (water temperature and elevation) considered in the study. Three principal components were retained and explained together 94.65 percent of the total 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  $\mu$ m.



**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 Hymenostomata. 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 *Glaucoides 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 bacterivory 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. gymnotrya* (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 caespitose 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.

**Acknowledgements:** To Dra. Blanca Pérez Uz, Universidad Complutense de Madrid for improving the manuscript. From Facultad de Ciencias, UNAM, to Biól. Margarita Reyes for their technical assistance in laboratory, to Mag. Daniel Espinosa Diaz for the statistical analysis, and to Mag. Aldi de Oyarzábal for the elaboration of the

**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 1</i>									+							1
<i>Peritrichia 2</i>			+													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.

scientific illustration. To Mag. Daniel Méndez for the elaboration of the map. We thank Mag. Adriana Rojas, Centro de Investigaciones Costeras La Mancha (CICOLMA), and Café La Onza for their permission to sampling. To Dr. W. Bourland, Boise State University, U.S.A. for his comments and English grammar revision.

## REFERENCES

- Benzing D. H. (2000) Bromeliaceae: Profile of an adaptive radiation. Cambridge University Press, New York
- Berger H. (1999) Monograph of the Oxytrichidae (Ciliophora, Hypotrichia). Monographiae Biologicae 78, Dordrecht
- Berger H. (2006) Monograph of the Urostyloidea (Ciliophora, Hypotrichia). Monographiae Biologicae 85, Dordrecht
- Borror A. C., Hill B. F. (1995) The order Euplotida (Ciliophora): taxonomy, with division of *Euplotes* into several genera. *J. Eukaryot. Microbiol.* **42**: 457–466
- Buosi P. R. B., Utz L. R. P., De Meira B. R., Segóvia da Silva B. T., Lansac-Tôha F. M., Tôha F. A. L., Velho L. F. M. (2014) Rainfall influence on species composition of the ciliate community inhabiting bromeliad phytotelmata. *Zool. Stud.* **53**: 32
- Buosi P. R. B., Cabral A. F., Utz L. R. P., Vieira L. C. G., Velho L. F. M. (2015) Effects of seasonality and dispersal on the ciliate community inhabiting bromeliad phytotelmata in riparian vegetation of a large tropical river. *J. Eukaryot. Microbiol.* **62**: 737–749
- Carrias J. F., Brouard O., Leroy C., Régis-Céréghino R., Pélozuelo L., Dejean A., Corbara B. (2012) An ant-plant mutualism induces shifts in the protist community structure of a tank-bromeliad. *Basic Appl. Ecol.* **13**: 698–705
- Carvajal-Hernández C. I., Krömer T. (2015) Riqueza y distribución de helechos y licofitos en el gradiente altitudinal del Cofre de Perote, centro de Veracruz, México. *Bot. Sci.* **93**: 601–614
- Clarholm M. (1985) Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. *Soil Biol. Bioch.* **17**: 181–187
- Curds C. R. (1975) A guide to the species of the genus *Euplotes* (Hypotrichida, Ciliata). *Bull. Br. Mus. Nat. Hist. Zool.* **28**: 1–61
- Czapik A. (1968) La famille Tetrahymenidae et son importance dans la systématique et l'évolution des ciliés. *Acta Protozool.* **5**: 315–357
- Dragesco J., Dragesco-Kernéis A. (1986) Ciliés libres de l'Afrique intertropicale. Introduction à la connaissance et à l'étude des ciliés. Faune tropicale vol. 26, Éditions de l'Orstom, Paris

- Dunthorn M., Stoeck T., Wolf K., Breiner H. W., Foissner W. (2012) Diversity and endemism of ciliates inhabiting neotropical phytotelmata. *System. Biodivers.* **10**: 195–205
- Durán-Ramírez C. A., Mayén-Estrada R. (2018). Ciliate species from tank-less bromeliads in a dry tropical forest and their geographical distribution in the Neotropics. *Zootaxa*. **4497**: 241–257
- Durán-Ramírez C. A., García-Franco J. G., Foissner W., Mayén-Estrada R. (2015) Free living ciliates from epiphytic tank bromeliads in Mexico. *Eur. J. Protistol.* **51**: 15–33
- Espejo-Serna A., López-Ferrari A., Ramírez-Morillo I. (2005) Bromeliaceae. *Flora de Veracruz* **136**: 1–307
- Fan X., Lin X., Liu W., Xu Y., Al-Farraj S. A., Al-Rasheid K. A. S., Warren A. (2013) Morphology of three new marine *Frontonia* species (Ciliophora; Peniculida) with notes on the phylogeny of this genus. *Eur. J. Protistol.* **49**: 312–323
- Fenchel T. (1980) Suspension feeding in ciliated protozoa: feeding rates and their ecological significance. *Microb. Ecol.* **6**: 13–25
- Foissner W. (1993) Colpodea (Ciliophora). G. Fischer Verlag, New York
- Foissner W. (1998) An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species. *Eur. J. Protistol.* **34**: 195–235
- Foissner W. (1999) Protist diversity: estimates of the near-imponderable. *Protist.* **150**: 363–368
- Foissner W. (2003) Morphology and ontogenesis of *Bromeliophrya brasiliensis* gen. n., sp. n., a new ciliate (Protozoa: Ciliophora) from Brazilian tank bromeliads (Bromeliaceae). *Acta Protozool.* **42**: 55–70
- Foissner W. (2006) Biogeography and dispersal of microorganisms: a review emphasizing protists. *Acta Protozool.* **45**: 111–136
- Foissner W. (2010) Life cycle, morphology, ontogenesis, and phylogeny of *Bromeliolithrix metopoides* nov. gen., nov. spec., a peculiar ciliate (Protista, Colpodea) from tank bromeliads (Bromeliaceae). *Acta Protozool.* **49**: 159–193
- Foissner W. (2013) Description of *Glaucoides bromelicola* n. gen., n. sp. (Ciliophora, Tetrahymenida), a macrostome-forming inhabitant of bromeliads (Bromeliaceae), including redescription of *Glaucoma scintillans* and *G. reniformis*. *J. Eukaryot. Microbiol.* **60**: 137–157
- Foissner W. (2014) An update of basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Int. J. Syst. Evol. Microbiol.* **64**: 271–292
- Foissner W. (2016) Terrestrial and semiterrestrial Ciliates (Protozoa, Ciliophora) from Venezuela and Galápagos. *Denisia*. **35**: 1–912
- Foissner W., Stoeck T. (2011) *Cotterillia bromelicola* nov. gen., nov. spec., a gonostomatid ciliate (Ciliophora, Hypotricha) from tank bromeliads (Bromeliaceae) with de novo originating dorsalkinetes. *Eur. J. Protistol.* **47**: 29–50
- Foissner W., Blatterer H., Berger H., Kohmann F. (1991) Taxonomische und ökologische revision des saprobiensystems. Band I: Cytrophorida, Oligotrichida, Hypotrichia, Colpodea. Informationsberichte des Bayer. Landesamtes für Wasserwirtschaft 1/91. München
- Foissner W., Strüder-Kypke M., Van Der Staay G., Moon-Van Der Staay S., Hackstein J. (2003) Endemic ciliates (Protozoa, Ciliophora) from tank bromeliads (Bromeliaceae): a combined morphological, molecular, and ecological study. *Eur. J. Protistol.* **39**: 365–372
- Foissner W., Wolf K. W., Yashchenko V., Stoeck T. (2011) Description of *Leptopharynx bromelicola* n. sp. and characterization of the genus *Leptopharynx* Mermod, 1914 (Protista, Ciliophora). *J. Eukaryot. Microbiol.* **58**: 134–151
- Lee J. J., Leedale G. F., Bradbury P. (1985) An Illustrated Guide to the Protozoa. Society of Protozoologists, Kansas
- Lynn D. H. (2008) The ciliated protozoa: characterization, classification, and guide to the literature. Springer, Dordrecht
- Maguire Jr. B. (1971) Phytotelmata: biota and community structure determination in plant-held waters. *Annu. Rev. Ecol. Syst.* **2**: 439–464
- Mondragon-Chaparro D., Villa-Guzmán D. M., Escobedo-Sarti G. J., Franco-Méndez A. D. (2006) La riqueza de bromelias a lo largo de un gradiente altitudinal en Santa Catarina Ixtepeji, Oaxaca, México. *Naturaleza y Desarrollo*. **4**: 13–16
- Moreno C. E. (2001) Métodos para medir la biodiversidad, Vol. 1. M&T-Manuales y Tesis SEA, Zaragoza
- Nadkarni N. M. (1994) Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Am. Zool.* **34**: 70–78
- Omar A., Foissner W. (2011) Description of *Leptopharynx bromeliophilus* nov. spec. and *Leptopharynx australiensis* nov. spec. (Ciliophora, Nassulida). *Acta Protozool.* **50**: 89–103
- Omar A., Foissner W. (2013) Description of two new *Drepanomonas* taxa and an account on features defining species in *Drepanomonas* Fresenius, 1858 (Ciliophora, Microthoracida). *Eur. J. Protistol.* **49**: 420–437
- Pomeroy L. R., Williams P. J., Azam F., Hobbie J. E. (2007) The microbial loop. *Oceanography*. **20**: 28–33
- Rahbek C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*. **18**: 200–205
- Rzedowski J. (1978) Vegetación de México. Limusa, México
- Weisse T. (2014) Ciliates and the rare biosphere-community ecology and population dynamics. *J. Eukaryot. Microbiol.* **61**: 419–433
- Weisse T., Scheffel U., Stadler W., Foissner W. (2013a) *Bromeliolithrix metopoides*, a boom and bust ciliate (Ciliophora, Colpodea) from tank bromeliads. *Eur. J. Protistol.* **9**: 406–419
- Weisse T., Scheffel U., Stadler P., Foissner W. (2013b) Functional ecology of the ciliate *Glaucoides bromelicola*, and comparison with the sympatric species *Bromeliolithrix metopoides*. *J. Eukaryot. Microbiol.* **60**: 578–587
- Wiackowski K., Kocerba-Soroka W. (2017) Selective predation by harpacticoid copepod on ciliates in phytotelmata: a laboratory experiment. *Hydrobiologia* **790**: 13–22

Received on 5<sup>th</sup> May, 2019; revised on 12<sup>th</sup> December, 2019; accepted on 11<sup>th</sup> February, 2020