



## MICROBIOLOGY

# “Hitchhiking with invertebrates”: two reports of epibiosis by peritrich ciliates on ostracods and hydrachnid mites in tanks of epiphytic bromeliads from south Brazil

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**Abstract:** Temporary waters are common environments found in physical and biological substrates. Among them, some bromeliads species are known to hold water in their tanks, in a habitat called phytotelmata. Phytotelmata serve as habitats for several organisms, from bacteria and protists to arthropods and anurans. Peritrich ciliates are often found as epibionts on aquatic invertebrates in these environments. Here, we report two cases of epibiosis involving *Lagenophrys* sp. attached to ostracods (*Elpidium* spp.) and *Rhabdostyla* sp. colonizing hydrachnid mites in the tanks of two bromeliad species. In our analysis, we measured the frequency of epibiosis considering the presence of both basibiont and epibiont in the samples. The results shown a significant difference between *Elpidium* sp. and *Lagenophrys* sp. compared to hydrachnid mites and *Rhabdostyla* sp. (87.5% and 19%, respectively), supported by the Kruskal-Wallis test ( $p = 0.0003$ , Chi-square = 9.687). These reports are important since the knowledge of phytotelmata communities from tropical and subtropical areas is incipient, although it has been increasing over the last years. It also shows that epibiosis doesn't always represent a beneficial relationship. These two epibiosis systems found in bromeliad tanks raise questions about organism's dispersal throughout other phytotelmata and other temporary water habitats.

**Key words:** Bromeliads, Epibiosis, Peritrich ciliates, phoresy, temporary waters.

## INTRODUCTION

Phytotelmata microhabitats harbor a high biodiversity and are models for natural experiments, receiving increasing interest by the scientific community (Teixeira et al. 2018). These microenvironments are model systems with a great diversity of organisms, where complex relationships (i.e., epibiosis) occur (Marino et al. 2011). In these environments, it is also possible to observe events of colonization, dispersion, competition, and prey-predator interactions (Siri et al. 2008). According to a scientometrics research by Teixeira et al. (2018), phytotelmata

hold a high diversity of biological communities, although there are still few studies focusing on these microhabitats. The most representative plant families that form phytotelmata are Bromeliaceae, Poaceae, and Apiaceae. Global concerns such as climate change and habitat fragmentation have attracted the attention to these environments in the recent years since they are reservoirs of biodiversity.

Bromeliads are considered temporary environments since they allow water to accumulate for different periods, serving as model organisms for natural experiments in

different ecological studies. Bromeliad leaves are arranged in rosettes and, at their bases, the storage of water and organic matter creates an environment suitable for several organisms. Organisms such as bacteria, protists, arthropods (insect larvae, crustaceans, mites), and frogs (Goffardi et al. 2015, Teixeira et al. 2018) have been reported colonizing bromeliad tanks. The colonization of these environments seems to be complex, involving interconnected sequential events, such as dispersion, arrival, and establishment of the organisms. Maguire (1971, 1963) described three mechanisms of dispersal of organisms in isolated bodies of water: wind and rain (passive), flight (active) and phoresy (introduction by another species). Bromeliads, in a comparative approach, can represent “suspended lakes” in a forest matrix, comparing the colonization process of the tanks with those that take place on islands (Frank & Lounibos 1987).

Considering that bromeliads have more than 3,000 species, with different habitats and morphologies, the diversity of ciliates that inhabits these environments remains poorly studied and underestimated (Foissner et al. 2003). Most bromeliad species are restricted to the Neotropics, and this type of phytotelmata provides evidence for the endemism and speciation of some ciliate species (Dunthorn et al. 2012). According to Foissner et al. (2003), two main categories of free-living ciliates inhabit bromeliad tanks: those that inhabit the mud and water column and those that live as epibionts attached to invertebrates. Peritrichia is a subclass of ciliates that include stalked and sedentary organisms, which may be solitary or colonial (Lynn 2008). These organisms are often observed as part of a relationship entitled epibiosis. This is an association between two organisms (epibiont-host or basibiont), and it is a common way of phoresy in nature (Cabral

et al. 2010). In this way, ciliates can use other organisms as dispersing agents to colonize new environments.

In isolated bodies of water, it is required to evaluate how dispersion processes occur. Some examples of hyperphoresy available in bromeliad tank environments are ostracods and annelids using the body of frogs to disperse to other bromeliads, and mites using birds and bumblebees (Lopez et al. 1999, 2005, García-Franco et al. 2001, Guerra et al. 2010, Araújo et al. 2019, Moroti et al. 2019). Some of these invertebrates are often carrying peritrich ciliates with them. Phoresy studies involving peritrich ciliates, on the other hand, are rare. Two cases of loricate ciliates represented by the genus *Lagenophrys* attached to ostracod shells were recorded by Sabagh et al. (2011), Jankowsk & Yankosvsky (2014) and Mestre et al. (2019) in Rio de Janeiro (Brazil), St. Petersburg (Russia), Iberian Peninsula and Balearic Islands (SW Europe) respectively. A recent study conducted by Chatterjee et al. (2018) has identified more than 10 species of peritrich ciliates living in both halacarid and hydrachnid mites, without specific preferences to their hosts. Other studies focusing on epibiosis and phoretic interactions in bromeliads or temporary bodies of water remain scarce.

## MATERIALS AND METHODS

During a fieldwork sampling bromeliad water across an altitudinal range (Malfatti et al. 2020), we observed two epibiotic relationships between ostracods and *Lagenophrys* sp., and mites and *Rhabdostyla* sp.. These relationships occurred in two different bromeliad species, in two different altitudes over a mountain range in Serra Geral, southern Brazil. The sampling sites were in Garapiá river (29° 30' S 50° 14' W) at 400 m above sea level (a.s.l.), and in RPPN Pró-Mata/

PUCRS (29° 29' S 50° 21' W), a private Protected Area owned by the Pontifícia Universidade Católica do Rio Grande do Sul, at 900m a.s.l.. Two sampling campaigns were carried out in each season: spring, summer, fall, and winter (total of 8 campaigns in each location), between October 2017 and September 2018. In both sites, bromeliad species in the genus *Vriesea* Gaudich. were chosen: *V. incurvata* was sampled in the Garapiá river, while *V. friburgensis* was sampled in Prô-Mata. We selected the bromeliad species based on their abundance in the study areas, and the presence of flower for correct identification.

The two bromeliad species were similar in size, in habit (both are epiphytes), and were at a maximum of 1.5m height above the ground. We sampled a total of 24 individuals from each species, three per campaign, randomly selected. In our original sample design, we collected fifteen milliliters of the central cistern water using a sterile Pasteur pipette and placed in Falcon tubes. We analyzed 8mL of *in vivo* samples to identify the species that composed the eukaryotic community, while the rest (7mL) were fixed in Lugol 10%. During the study period, we found the peritrich ciliate *Lagenophrys* sp. attached to specimens from the ostracod genus *Elpidium* in the tanks of *V. incurvata*. In *V. friburgensis*, we observed different species of Hydrachnidae mites carrying the peritrich genus *Rhabdostyla*. These epibiotic relationships were present in many samples analyzed and we estimated the frequency of their occurrence.

## RESULTS

The *Lagenophrys* sp./*Elpidium* sp. epibiotic system occurred in 58.3% of all analyzed samples, whereas the *Rhabdostyla* sp./Hydrachnidae mite relationship was observed in 16.7%. Ostracods carrying *Lagenophrys* sp. were present in all seasons, while *Rhabdostyla*

sp. colonized mites during spring, summer, and winter. We also observed *Rhabdostyla* spp. as free-living individuals, occurring over debris and organic matter in our study. *Lagenophrys* has a higher prevalence on ostracod shells, with 5 to 6 individuals attached to each basibiont. Individuals of *Rhabdostyla* sp. were observed colonizing specially the legs of mites.

In our analysis, we measured the frequency of epibiosis considering the presence of both basibiont and epibiont in the samples. We tested if the frequency of these relationships were different, and their seasonal variance. The results shown a significant difference between *Elpidium* sp. and *Lagenophrys* sp. epibiosis than Hydrachnidae mites and *Rhabdostyla* sp. (87.5% and 19%, respectively), supported by the Kruskal-Wallis test ( $p = 0.0003$ , Chi-square = 9.687) (Table I).

This difference is also reflected throughout the seasons, where *Elpidium* sp. and *Lagenophrys* sp. occurred at all seasons, and had a higher frequency in the samples, varying from 83.3% to 100%. Hydrachnidae mites and *Rhabdostyla* sp. were present in spring, summer and winter (33.3%, 20% and 20%, respectively).

## DISCUSSION

Our report supports a close association between ostracods and *Lagenophrys* sp.. We assume that ostracods are potential dispersers of *Lagenophrys* sp. between bromeliad tanks, and probably to other temporary pools, where they inhabit. One of the reasons may be the presence of the ostracod bivalve shell, which provides a hard protective substrate for the host, and a large area for epibiont attachment. Apparently, the epibiont load did not affect the swimming behavior of the ostracods, which could favor dispersion. Without movement impairment of the host, epibionts could be dispersed for

**Table I. Total frequency (%) of both epibiosis systems and throughout the seasons.**

	Frequency of epibiosis (%)	
	<i>Elpidium</i> sp. and <i>Lagenophrys</i> sp.	Mite and <i>Rhabdostyla</i> sp.
Spring	100	33.3
Summer	83.3	20
Autumn	83.3	0
Winter	100	20
Total	87.5	19
* considering the presence of both basibiont and epibiont in the samples.		

long distances, and even “hitchhike” when the ostracods are being transported by frogs, lizards, or snakes (Lopez et al. 1999). As for *Rhabdostyla* sp., even if the epibiont is affecting host movement, and this effect depends on the epibiont load, host and epibiont might be dispersed when carried by other animals (García-Franco et al. 2001, Guerra et al. 2010, Araújo et al. 2019, Moroti et al. 2019).

Some studies have related epibionts specificity to hosts at family, genus, and even species level (Cook & Chubb 1998, Nenninger 1948). The frequency of *Lagenophrys* sp. living on ostracod shells in our samples indicate a preference of the peritrich ciliate for this living substrate. Lagenophryids are well known as obligate symbionts of some crustaceans, predominantly in freshwater, occurring on the gills, legs or in the integument of their hosts (Corliss & Brough 1965). The majority of species have been reported as epibionts on amphipods, although cladocerans, ostracods, copepods, and isopods have also been reported as hosts (Kahl 1935, Shomay 1953, Clamp 1973).

According to Clamp (1973), *Lagenophrys* spp. filter their food by the currents created by respiratory or locomotory activities of the hosts, which reinforces the obligatory association these peritrichs have with their hosts. Shomay (1955) discussed that the restriction of epizoic ciliates of some crustaceans relates to the affinity of the hosts’ exoskeletons with epibiont

properties. According to Mayén-Estrada & Clamp (2016), lagenophryids are usually flattened along its oral-aboral axis, and attaches to surfaces with the base of the lorica, and it may be attracted by physical (thigmotactic) or chemical (chemotactic) signals. These signals may allow the epibiont to detect small differences in the exoskeletons of different crustaceans (Clamp 1973). Studies analyzing host attributes and areas for attachment considered feeding behavior (Fernandez-Leborans & Gabilondo 2006), protected areas (Fernandez-Leborans 2003), trophic differences (Clamp 2005), less active parts (Utz & Coats 2005), and availability of respiratory or filter feeding currents (Arndt et al. 2005). Considering their association with ostracods, the shells of *Elpidium* spp. seems to offer a suitable and secure surface to attach.

It is worth mentioning that *Elpidium* species are distributed mostly in temporary water environments (Little & Herbert 1996). Some reproductive characteristics of these species are adapted to the typical ephemerality of phytotelmata and similar habitats. To deal with the stressful conditions of these environments, both basibiont and epibiont may develop adaptative mechanisms of reproduction related to drought and wet periods (Foissner 2003, Halberg et al. 2013, Buosi et al. 2015). Studies relating their reproductive response to different seasons are needed to elucidate these questions.

*Rhabdostyla* spp. are extensively listed in the literature in epibiosis with different metazoan groups such as rotifers, copepods, mites, annelids, and even Diptera, Ephemeroptera, and Odonata larvae (Cabral et al. 2016, Chatterjee et al. 2018, Corbi et al. 2017, Dias et al. 2007). Despite being widely observed as epibionts, these peritrich ciliates are also often found as free-living forms in different habitats (Patterson 1992). Although there was a low frequency of this epibiotic relationship with mites, the colonization rate was high with a mean of four to six individuals per host. In this case, there was a clear impairment of the host's movement due to the heavy epibiont load. Effects of epibionts on the host movements was also reported by Henebry & Ridgeway (1979), where peritrich ciliates were found at any point on their host where they would not sustain damage from the organism's swimming and feeding activities. Epibiosis can also negatively affect basibionts by increasing weight and friction, decreasing flexibility, or shading basibionts from light and access to dissolved molecules (Wahl & Mark 1999). According to Corbi et al. (2017), the relationship is more beneficial to the epibiont since they can often improve their dispersal capability or reach nutrient-rich and more oxygenated spots.

Water mites (Hydrachnidae) present interesting biological and ecological aspects related to reproduction, feeding, and development. Both adults and deutonymphs are predators, sucking the preorally digested fluid or insect eggs (Böttger 1970, Proctor & Pitchard 1989, Smith & Cook 1991). They reproduce sexually, although there are cases of parthenogenesis (especially in phytotelmata habitats due to the stressful environments), which explains the unbalanced sex ratios of some assemblages (Baker 1991, Proctor 1996). Since they are active predators, epibiosis could cause friction in their

displacement, affecting the host's survival. In our study, during the analyses of living samples, mites seemed to move slowly due to the epibiont load, which may explain the low frequency of the epibiosis with *Rhabdostyla* sp..

Kwet et al. (2010) published a guide with 56 species of amphibians from Pró-Mata and other areas of the mountain forests of Serra Geral of south Brazil. The bromeliads sampled in our study were inserted in Atlantic forests that harbored a great diversity of herpetofauna. Few examples of phoresy considering the environment of the bromeliads is ostracods and annelids using the body of frogs to disperse and to move to among bromeliads (Lopez et al. 1999, 2005). Sabagh and collaborators (2011) found that the anurans carrying ostracods has ciliates from the genus *Lagenophrys* sp. attached on their shells. We suggested that "hyperphoresy" may be occurring, where *Lagenophrys* can "hitchhike" with *Elpidium* ostracods, which in turn may be transported to other bromeliads by serpents and amphibians. Since mites and *Rhabdostyla* sp. had a weaker association, maybe hyperphoresy doesn't contribute to their dispersal.

We observed a higher prevalence of ostracods with *Lagenophrys* sp. during spring. Maybe there is a seasonal influence on this epibiosis related to flowering event of the bromeliads. Negrelle & Muraro (2006) found that the flowering peak period of *V. incurvata* occurs during spring. According to Araujo et al. (1994) the hummingbird species *Ramphodon naevius* is responsible for pollination in *V. incurvata* and other *Vriesea* species. Although phoretic relationships of ostracods is well documented with amphibians, these crustaceans could also "hitchhike" on birds in non-marine environments (Green & Figuerola 2005). In this case, the flowering event of *V. incurvata* during spring could indicate higher presence

of pollinators visiting bromeliads, which may increase dispersion of *Elpidium* sp., leading to an increase in abundance during this season. Bromeliaceae is one of the few families of plants that are pollinated predominantly by birds rather than insects, and hummingbirds pollinate most species of this family (Smith & Downs 1974, Sick 1997). In this case, pollinators may be helping in the dispersion of ostracods and their epibionts across different bromeliad individuals.

According to Cook & Chub (1998), epibiosis can be a facultative, opportunistic, and non-specific relationship. Epibiosis has major effects on the species involved and on community structure and dynamics. Coevolution can be expected when this relationship leads to a specificity of both basibiont and epibiont, although current evidence suggests that many epibionts are generalists regarding the substratum they use (Wahl & Mark 1999). In nature, epibiosis have been studied for a long time, although there is a large gap in the knowledge about the colonization of zooplankton by epibionts in tropical and subtropical systems (Regali-Selegim & Godinho 2004). In phytotelmata habitats, the knowledge of biodiversity is increasing and, consequently, more can be discovered about these relationships. In our study, the two epibiotic systems showed different intensities of association between the species involved.

This report focused on the association between invertebrate hosts and their epibionts, considering the obligate condition of the relationship and discussing the potential role of the hosts as dispersers of the ciliates. Results that pointed out a strong fluctuation and association between the frequency of epibionts and hosts, like *Elpidium* sp. and *Lagenophrys* sp., have indicated a well-established relationship. In these cases, the peritrich ciliate have a

stable living substrate to attach and can have its dispersion linked to the phoresy of its hosts. The presence of an epibiont not always produce beneficial or neutral effects on its host. The epibiotic relationship between Hydrachnidae mites and *Rhabdostyla* sp. observed in this study could raise questions on how epibiotic relationships may bring negative effects to their hosts, affecting their capacity of dispersal and even survival, making this genus of peritrich ciliate a possible ectoparasite. This should be considered when studying the interactions between host-epibiont in any epibiotic relationship.

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