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Revisão

Ascogregarina (Apicomplexa: Lecudinidae): An overview of its distribution and pathogenicity on *Aedes aegypti* and *Ae. albopictus* development

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Resumo

Visão geral da distribuição de *Ascogregarina* (Apicomplexa: Lecudinidae) e seu papel no desenvolvimento biológico de *Aedes aegypti* e *Ae. albopictus*. As ascogregarinas são protozoários, pertencentes ao filo Apicomplexa, que parasitam várias espécies de invertebrados, incluindo algumas importantes espécies de mosquitos envolvidas na transmissão de arboviroses, como dengue, febre amarela, chikungunya e zika. As espécies gregarinas mais frequentemente reportadas em mosquitos são *Ascogregarina culicis*, *A. taiwanensis* e *A. barreti*, as quais possuem *Aedes aegypti*, *Ae. albopictus* e *Ae. triseriatus* como hospedeiros naturais, respectivamente. Estudos têm demonstrado que o parasitismo de algumas espécies de *Ascogregarina* pode influenciar negativamente o desenvolvimento biológico desses mosquitos e tal influência depende da sua distribuição ambiental. Assim, nesta revisão, foi verificada a distribuição de espécies de *Ascogregarina* em vários países, bem como sua influência no desenvolvimento de mosquitos e seu possível uso como controle destes insetos.

Palavras-chave: Arboviroses; Controle de mosquitos; Parasitismo

Abstract

Ascogregarina species are protozoa that belong to the phylum Apicomplexa and parasitize several species of invertebrates, including some important mosquito species involved in transmitting arboviruses, such as dengue, yellow fever, chikungunya and Zika virus. The most frequent gregarine species reported for mosquitoes are

Ascogregarina culicis, *A. taiwanensis* and *A. barreti*, which have *Aedes aegypti*, *Ae. albopictus* and *Ae. triseriatus* as natural hosts, respectively. Studies have shown that parasitism by some *Ascogregarina* species can negatively influence the biological development of mosquitoes and that this influence depends on their environmental distribution. In this review, we revise the distribution of *Ascogregarina* species in several countries and discuss how these parasites influence the development of mosquitoes and could possibly be used as a mosquito control.

Key words: Mosquito control; Parasitism; Vector-borne diseases

Introduction

Some mosquito species, such as *Aedes aegypti* Linnaeus and *Ae. albopictus* Skuse, are globally important vectors of diseases and are responsible for transmitting arboviruses, such as dengue, yellow fever, chikungunya (GUBLER, 2011; STAPLES; FISCHER, 2014), Mayaro virus (VIEIRA et al., 2015), and Zika virus (CHOUIN-CARNEIRO et al., 2016). Dengue is considered one of the most important arboviruses due to high morbidity and mortality, and because of large epidemics in several regions around the world, especially in tropical and subtropical countries (GUZMAN; HARRIS, 2015). The chikungunya virus has also caused serious epidemics in various parts of the world and, in most cases, its symptoms are very similar to dengue. However, sometimes the infection causes strong inflammation in the joints that leads to severe pain in the patient due to persistent arthralgia (MONTERO, 2015; WEAVER; FORRESTER, 2015). Arthralgia can also be the most severe and prominent manifestation of a Mayaro virus infection, which is found in South America (VIEIRA et al., 2015).

More recently, another neglected arthropod virus, called the Zika virus, emerged in Brazil in 2015. Since then, this disease has spread rapidly within the Americas, giving rise to several cases of congenital malformations and neurological syndromes (HEUKELBACH et al., 2016).

Both *Ae. aegypti* and *Ae. albopictus* are distributed worldwide, from tropical to temperate climates, and occupy all of Brazil (KRAEMER et al., 2015) where millions of dengue, chikungunya and Zika outbreaks have been reported annually, mainly in the Northeast Region of the country. Another important species responsible for transmitting arboviruses is *Ae. triseriatus* Say. This is an invasive mosquito species that is prevalent in the United States, where it is responsible for transmitting the La Crosse virus (JONES et al., 1999; BORUCKI et al., 2001; WESTBY et al., 2015). However, this species has been recently reported in Mexico (SÁNCHEZ-TRINIDAD et al., 2014). A study conducted by Trout Fryxell et al. (2015) demonstrated the natural infection of *Ae. triseriatus* by the La Crosse virus based on larvae collected in a cemetery that were screened for LACv using RT-PCR.

The ability of *Ae. triseriatus* to utilize artificial container habitats for larvae development, like *Ae. aegypti* and *Ae. albopictus,* suggests that this species could easily become established in Latin America.

Controlling the vectors is the main method used to avoid arboviruses, which can be done by naturally managing artificial breeding places of mosquito larvae. A second method is to apply biological and chemical products when using integrated management in environmental programs (SALOKHE et al., 2012; SILVA et al., 2013; ARAÚJO et al., 2015; CAIXETA et al., 2016). Among these applications, chemical control may promote the selection of resistant populations (PROPHIRO et al., 2011; BELLINATO et al., 2016; SMITH et al., 2016) and cause other problems, such as adverse effects on non-target organisms, high cost and environmental damage, since most applied insecticides are not biodegradable (BLAIR et al., 2000). Environmentally friendly alternatives have been explored to help reduce the selection pressure for insecticide resistance. Biocontrol strategies include natural organisms that exploit mosquito behaviour to increase mosquito mortality and releasing mosquitoes that are either sterile or unable to transmit disease (BENELLI et al., 2016). This control method is advantageous because it employs organisms that have target specificity, does not cause environmental pollution and has a lower risk of selecting resistant populations (GARCIA et al., 2016). Some examples of biocontrol strategies are growth regulators that act through chitin synthesis inhibitors, and behaviour modifiers that can be generated by viruses, bacteria, fungi, and protozoa (LELES et al., 2012; LU et al., 2012; OTTA et al., 2012; SILVA et al., 2013). As demonstrated, *Ae. aegypti* and *Ae. albopictus* are potential vectors of a number of arboviruses. Each of these mosquito species can naturally harbour a specific gregarine parasite that allows the host mosquito to carry out life functions while remaining relatively unaffected by its presence (MORALES et al., 2005). Among these protozoa, some species of *Ascogregarina* are highly prevalent in natural populations of some mosquito species (BLACKMORE et al., 1995). The most studied species are *A. taiwanensis*, *A. culicis* and *A. barreti*, which parasitize *Ae. Albopictus*, *Ae. aegypti* and *Ae. triseriatus*, respectively.

Gregarines

The phylum Apicomplexa, which includes *Ascogregarina* spp., is represented by obligate protozoan parasites. Their invasive form is characterized by the presence of a single apical complex responsible for penetration and cell invasion (MORRISON, 2009), usually in the intestine, coelom and reproductive tissues of invertebrates (LEANDER, 2008). The genera *Ascogregarina* (syn. *Monocystis* von Stein, *Lankesteria* Mingazzini and *Ascocystis* Grasse) and *Psychodiella* (Eugregarinorida: Aseptatorina) have recently been included in the new family Ascogregarinidae. Previously, species that parasitize mosquitoes and sandflies belonged to a single genus: *Ascogregarina* (DESPORTES, 2013). However, recently, they were placed in two genera: (1) *Ascogregarina,* represented by species that parasitize mosquitoes, flies and fleas; and (2) *Psychodiella,* represented by species that parasitize sandflies (LANTOVA; VOLF, 2014). The classification using trophozoites is based on parasite habitats, host diversity and morphological characteristics (VIVIER; DESPORTES, 1990).

It is estimated that there are many unknown species that parasitize different invertebrate hosts (CLOPTON, 2000; HAUSMANN et al., 2003; DESPORTES, 2013). Host species of terrestrial gregarines have mostly been reported to be insects, including aquatic insects, coleopterans and dipterans (VOTÝPKA et al., 2009). Until now, few species of *Ascogregarina* that parasitize mosquitoes have been described (BEIER; CRAIG, 1985; CHEN, 1999; LANTOVA; VOLF, 2014). The most well-known species are *A. culicis*, *A. taiwanensis* and *A. barretti* (Table 1). These species are morphologically similar, except for the size and shape of their oocysts and gamonts (ROYCHOUDHURY; KOBAYASHI, 2006).

TABLE 1: Reports about worldwide distribution of *Ascogregarina* species in wild populations of mosquitoes.

***Ascogregarina* species**	**Host species**	**Oocyst length**	**Trophozoite length**	**Country**	**Reference**
		5-10 µm	*	Taiwan	Lien and Levine (1980)
		*	*	USA	Reinert (2000)
		*	*	USA	Blackmore et al. (1995)
		8.3-9.9 µm	*	USA	Garcia et al. (1994)
		8.72 µm	*	Taiwan	Chen et al. (1997)
A. taiwanensis	*Ae. albopictus* (Skuse)	*		USA	Comiskey (1999)
		*	*	USA	Reyes-Villanueva et al. (2003)
		9.9 µm	*	Japan	Roychoudhury et al. (2007a)
		*	80 µm	Brazil	Passos and Tadei (2008)
		*	50-621 µm	Brazil	Prophiro et al. (2017)
		*	*	Mexico	Reyes-Villanueva et al. (2013)
	Ae. aegypti (Linnaeus)	*	*	USA	Garcia et al. (1994)
		*	*	Brazil	Prophiro et al. (2017)

A. culicis		6 µm	*	India	Ross (1898)
		*	*	USA	Hayes and Haverfield (1971)
		*		India	Beier et al. (1995)
		*	*	Brazil	Marchoux et al. (1903)
		10-12 µm	*	*	Vavra (1969)
		11 µm	*	*	Lien and Levine (1980)
	Ae. aegypti (Linnaeus)	*	*	USA	Blackmore et al. (1995)
		*	*	India	Beier et al. (1995)
		9.5-12.2 µm	*	Argentina	Dellape et al. (2005)
		*	*	USA	Reyes-Villanueva et al. (2003)
		10.6-11.4 µm	*	Argentina	Vezzani and Wisnivesky (2006)
		*	76.9-116.5 µm	Argentina	Albicócco and Vezzani (2009)
		*	60 µm	Brazil	Passos and Tadei (2008)
		8.8 µm	*	Not cited	Roychoudhury et al. (2007a)
	Ae. geniculatus (Olivier)	12 µm	*	England	Ganapati and Tate (1949)
		11 µm	150-310 µm,	USA	Vavra (1969)
A. barrenti	*Ae. triseriatus* (Say)	*	*	USA	Beier and Harris (1983)
		*	*	USA	Porter and Defoliar (1985)
		*	*	USA	Blackmore et al. (1995)
		*	*	USA	Comiskey et al. (1999)
		*	*	USA	Van Rhein et al. (2000)
A. tripteroidesi	*Tripteroides dofleini* (Guenther)	*	*	Sri Lanka	Guenther (1914)
		*	*	India	Bhatia (1938)
A. clarki	*Ae. sierrensis* (Ludlow)	10-12 µm	129.1 µm	USA	Sanders and Poinar (1973)
A. lanyuensis	*Ae. alcasidi* (Huang)	9 µm	190 µm	Taiwan	Lien and Levine (1980)
A. armigerei	*Armigeres subalbatus* (Coquillett)	14.5 µm	*	Taiwan	Lien and Levine (1980)
		13.2 µm	*	*	Roychoudhury et al. (2007a)
A. geniculati	*Ae. geniculatus* (Olivier)	9-11 µm	*	Czech Republic	Kramar (1952)
		13.5 µm	*	Italy	Munstermann and Levine (1983)
A. polynesiensis	*Ae. polynesiensis* (Marks)	9.32 µm	35-65 µm	Independent State of Samoa	Pillai et al. (1976)
A. japonicus	*Ochlerotatus japonicus* (Theobald)	*	*	Japan	Roychoudhury et al. (2007b)

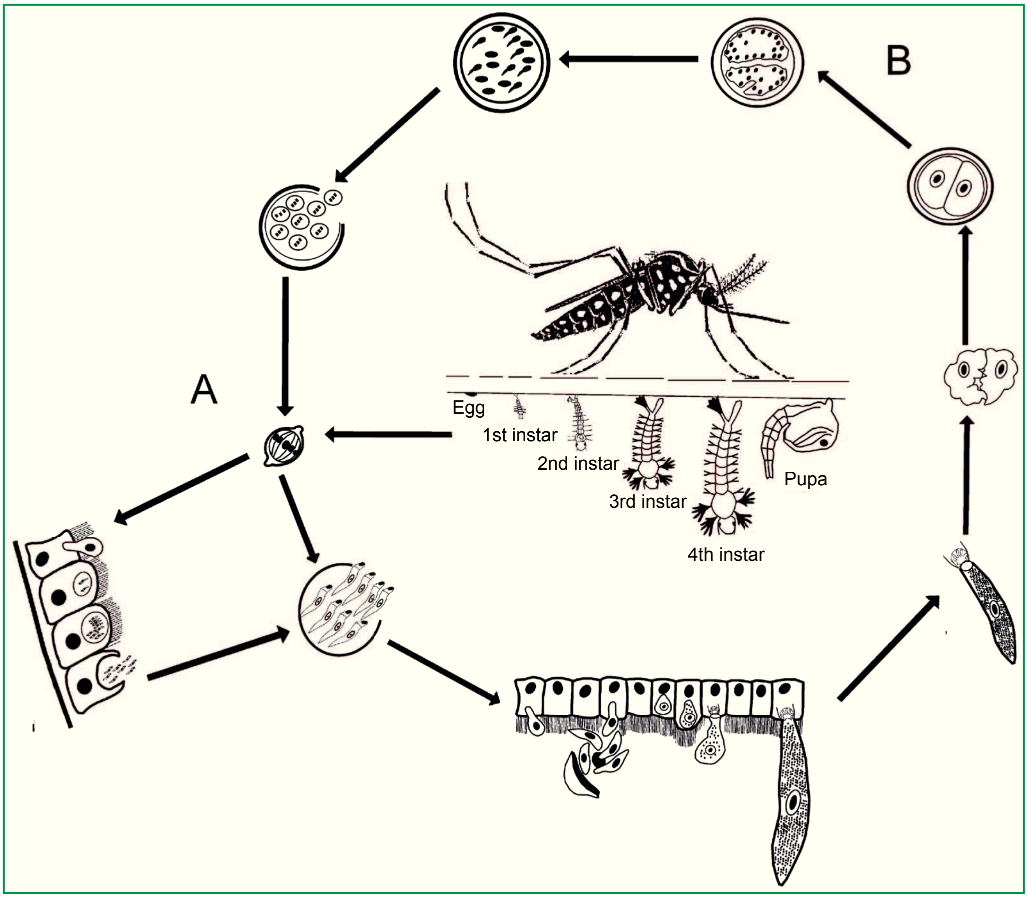
* Not mentioned

The life cycle of *Ascogregarina* spp.

The life cycle of *Ascogregarina* spp. is based on *A. taiwanensis* and *A. culicis*, since they are the most studied species that parasitize mosquito vectors. The life cycle of gregarines is similar between these two species and begins with the ingestion of mature oocysts by an invertebrate host (CHEN, 1999; TSENG, 2007).

In this work, the description is based on the relationship between *A. taiwanensis* and *Ae. albopictus* (Figure 1). The asexual cycle begins when oocysts that contain sporozoites are ingested by mosquito larvae. After a few minutes, sporozoites are released and undergo an intracellular phase in the epithelial cells of the foregut (ROYCHOUDHURY; KOBAYASHI, 2006). In different hosts, they can also invade other organs, such as the coelom and reproductive tissues (BEIER; CRAIG, 1985; LEANDER, 2008). After a short intracellular phase, sporozoites leave the epithelial cells to form extracellular trophozoites that fix themselves to the epithelium by their epimerites (CHEN et al., 1997). These trophozoites are found mostly in a posterior portion of the midgut, where vacuolar H+ATPase (V-ATPase) is actively expressed (HUANG et al., 2006). The trophozoites of *A. taiwanensis* in the midgut of mosquito larvae normally mature alongside host development (CHEN; YANG, 1996). Based on molecular markers, Chen (1999) observed that only 50% (or less) of *A. taiwanensis* trophozoites successfully migrate. An ultra-structural study made by Chen et al. (2013) showed that trophozoites that failed to migrate were retained in the midgut of mosquito pupae. The rest generally die by necrosis or apoptosis (KANDUC et al., 2002). Chen et al. (2013) also observed degradation of chromosomal DNA and detection of caspase-like activity. DNA fragmentation also appeared in extracted

FIGURE 1: The asexual (A) and sexual (B) reproduction life cycle of *Ascogregarina taiwanensis* parasitizing *Aedes albopictus*; 1: trophozoite stage; 2-5: gamete fusion, gametocyte and oocyst formation; 6: release of oocysts; 7: oocysts; 8: sporozoites. Modified from Vivier and Desportes (1990).



genomic material, implying that apoptosis occurred in most, if not all trophozoites that did not successfully migrate.

When mature trophozoites develop into gamonts in the midgut lumen of larvae, as well as in the pupal stage, they migrate to Malpighian tubules due to their gliding motility, where their sexual cycle (gametogony) and posterior fusion of gamonts occurs (WETZEL et al., 2003). Migration of *Ascogregarina* spp. from the midgut to Malpighian tubules is unidirectional and generally occurs between the trophozoites that were released in the midgut of early pupae, usually five hours after pupation (CHEN; FAN-CHIANG, 2001). The size of mature gamonts is extremely variable and dependent on the host and its geographic distribution (GARCIA et al., 1994). Sexual reproduction results in the formation of gametocysts, wherein true gametes are formed by nuclear division and cytokinesis. Fertilization occurs by the fusion of two gametes in the gametocyst, resulting in oocyst production with eight sporozoites (CHEN et al., 1997).

The possible routes for dissemination of the parasite occur when pupae or emerged adult mosquitoes infected with oocysts die at the site of reproduction, or when oocysts are released when adults emerge. The transmission can also occur at the time of oviposition, when infected females release oocysts together with their eggs (BEIER; CRAIG, 1985; LEANDER, 2008).

In most *Ascogregarina* species, oocysts can persist 4-6 months (on average) without water (ROYCHOUDHURY; KOBAYASHI, 2006). Chen and Yang (1996) showed that under laboratory conditions the optimum temperature for *A. taiwanensis* development is 24ºC. They observed that a temperature as high as 29ºC shortened the development period of this parasite, and most oocysts failed to mature. In addition, gametocysts did not form if the mosquito remained in the larval stage at 14ºC, indicating that the development of the parasite may also be influenced by host hormone levels.

Identification of *Ascogregarina* spp.

In terms of *Ascogregarina* parasites of mosquitoes, Comiskey et al. (1999) stated that *A. barretti*, *A. culicis*, and *A. taiwanensis* could sometimes occur in the same breeding places. Although *A. barretti* trophozoites can be visually distinguished from the other two parasite species in mosquito midgut infections, it is difficult to distinguish between *A. taiwanensis* and *A. culicis* because they have a similar size and morphology (Lien and Levine 1980). Thus, an accurate identification is necessary, mainly because these parasites can sometimes parasitize both *Ae. aegypti* and *Ae. albopictus*.

Beier and Harris (1983) evaluated the cross infection of *A. barretti* and *A. geniculate* in *Ae. triseriatus* under laboratory conditions. To distinguish these gregarine species, the authors subjected them to isoenzyme electrophoresis. The isocitrate dehydrogenase bands of each were clearly distinguishable on the same electrophoretic track. This technique appears to be a reliable method for resolving taxonomic complications of gregarines in mosquitoes.

Since oocysts are the only free-living stage of *Ascogregarina* parasites, and it is not easy to identify a difference in size among species, it is quite difficult to identify the parasites based solely on microscopic observations of oocysts. Therefore, studies to identify these parasites using subunit ribosomal DNA (SSU rDNA) have proved to be highly informative for phylogenetic studies and species identification (ROYCHOUDHURY et al., 2007a).

Reyes-Villanueva et al. (2001) described morphological characteristics to determine *Ascogregarina* spp. using gamonts of *A. taiwanensis*. They have a yellow granular cytoplasm, visible using phase-contrast microscopy, while those of *A. culicis* have a crystalline cytoplasm. However, according to Morales et al. (2005), morphological differentiation of gamonts involves dissection, which requires considerable technical skill and careful timing to reliably view extracellular gamonts. On the other hand, this may not always be reliable when dealing with mosquito larvae collected in the field, which can consume oocysts of both gregarine species at different times during larval development, resulting in trophozoites and gamonts of varying ages in an individual larva. Blackmore et al. (1995) already described such difficulties in identifying *A. taiwanensis* and *A. culicis* parasitizing *Ae. aegypti* and *Ae. albopictus* competing in the same breeding places. Based on these reports, Morales et al. (2005) developed specific primers for identifying *Ascoregarina* species using PCR. This technique was very useful for confirming that *Ae. aegypti* and *Ae. albopictus,* collected in southern Brazil, harboured *A. taiwanensis* (PROPHIRO et al., 2017).

Pathogenicity of *Ascogregarina* spp. during mosquito development

Among the reported species, *A. taiwanensis*, *A. culicis* and *A. barretti* are the most frequent parasites of mosquitoes in several countries (REEVES, 2004). Various authors have reported that these parasites have low or no pathogenicity on their natural hosts (WALSH; OLSON, 1976; BEIER; CRAIG, 1985; COPELAND, CRAIG; 1992; YEH et al., 1994). Furthermore, some authors suggest that their pathogenicity may vary according to the geographical distribution of vectors.

Barrett (1968) was the first author to report that *A. culicis* is highly pathogenic to *Ae. aegypti*. After this report, several surveys and tests were conducted in the United States in order to verify the potential role of *A. culicis* for the biocontrol of *Ae. aegypti,* since a strain of *A. culicis* originating from the United States is considered non-pathogenic (BARRETT, 1968). In observations made by McCray et al. (1970) in Georgia, USA, *A. culicis* did not affect larval development, size, mortality, pupal weight and adult emergence of *Ae. aegypti*. However, Barrett et al. (1971) observed that *A. culicis* had an adverse effect on *Ae. aegypti* by reducing host fecundity. Gentile et al. (1971) studied the distribution of *A. culicis* parasitizing *Ae. aegypti* by the distribution of oocysts in the USA. They observed that the parasites apparently had few deleterious effects on the host populations. Hayes and Haverfield (1971) conducted a survey in Florida, USA, and suggested that *A. culicis* did not exert a serious limiting effect on *Ae. aegypti* populations. Stapp and Gasten (1971) also inspected *Ae. aegypti* larvae for infection with *A. culicis* throughout cities in Florida. Generally, larvae infection was not high. The authors suggested that the levels of *A. culicis* infection in *Ae. aegypti* larvae could be increased by introducing parasite sporocysts into potential breeding containers.

On the other hand, four strains of *A. culicis* from Thailand were pathogenic to *Ae. aegypti,* causing atrophy and increased mortality of larvae and pupae (SULAIMAN, 1992). In Malaysia, this author evaluated the susceptibility of three strains of *Ae. aegypti* to four strains of *A. culicis* under laboratory conditions. The parasite was found to be pathogenic to the mosquito, the level of pathogenicity varied among geographical strains of *A. culicis,* and susceptibility varied among geographical strains of *Ae. aegypti*. In addition, infection with the parasite was found to shorten the mosquito larval development time.

In relation to *Ae. albopictus,* Comiskey et al. (1999) observed that *A. taiwanensis* collected in New Orleans, USA, negatively influenced the performance of this mosquito species only when larvae were poorly fed. According to Munstermann and Wesson (1990), *Ae. albopictus* is often heavily parasitized by *A. taiwanensis*. These protozoan parasites have been frequently described as having different levels of pathogenicity on their natural hosts (WALSH; OLSON, 1976; BEIER; CRAIG, 1985; COPELAND; CRAIG, 1992). Garcia et al. (1994) studied the prevalence of *A. taiwanensis* in larvae of *Ae. albopictus* and found minimum values (68%) in April, which increased to a maximum (100%) in August and then decreased in the winter.

Pathogenic effects on hosts are probably related to the negative impact on tissues where parasites develop. When mosquito larvae are infected, the epithelial cells of the intestine extend their nucleus and can be destroyed by the parasites (KRAMAR, 1952; SANDERS; POINAR, 1973). Moreover, Malpighian tubules in adults become swollen (WENYON, 1911) and their cells become distorted and damaged (BARRETT, 1968; MCCRAY et al., 1970; SANDERS; POINAR, 1973). Furthermore, Barrett (1968) showed that the extent of this damage is proportional to the infection rate of parasites.

Under stressful conditions, *A. taiwanensis* increases larval mortality of *Ae. albopictus*, decreases female fecundity, prolongs male and female development (COMISKEY et al., 1999), and reduces *A. albopictus* oviposition and hatch rate (YEH et al., 1994).

Prophiro (2013) analysed the influence of parasitism of *A. taiwanensis* on the biological development of the natural host *Ae. albopictus* under laboratory conditions. This author showed that the infected population had a lower survival rate, viability/hatching and number of eggs compared to the uninfected population.

Aedes triseriatus is a vector of the La Crosse encephalitis virus in North America (WESTBY et al., 2015). This species is commonly infected by *A. barretti* (WALKER et al., 1987). According to Craig (1993), their larvae can be found in tree holes, discarded tires, and other containers. Beier and Harris (1983) reported that 62% of the larvae and 35% of the adults collected from tree holes and discarded tire habitats in northern Indiana were infected by *A. barretti*. They also observed that parasitism of *Ae. triseriatus* by *A. barretti* extends the time of pupae development in males and diminishes pupae size of females, but induces no effect on larval survival, emergence or survival of adults. Similarly, Van Rhein et al. (2000) described that when *A. barretti* parasitizes *Ae. triseriatus,* female fecundity and size is reduced. Moreover, Porter and DeFoliart (1985) collected *A. triseriatus* in southern Wisconsin and found that 39% of adult females were infected by *A. barretti*. Also, Beier and Harris (1983) suggested that *A. barretti* is a relatively benign parasite of *Ae. triseriatus*. This author observed that infection did not affect larval mortality, adult emergence, or adult survival of *Ae. triseriatus*. However, it produced some slight effects on female pupal weight and male development time under laboratory conditions. Porter and DeFoliart (1985) found more frequent infections in nulliparous than parous *Ae. triseriatus,* but this difference cannot be definitively attributed to parasitism because mosquitoes may shed spores during oviposition.

Spencer and Olson (1982) observed low rates of egg hatching, larval survival and reduction in parasitized female weight in *Ae. hendersoni*, which is a non-natural host of *A. barretti*.

Garcia et al. (1994) observed that the level of pathogenicity in mosquitoes by a gregarine is not only influenced by sex and nutrients, but also because the parasite may be significantly more pathogenic when it is introduced in a non-natural host (e.g., when *A. taiwanensis* infects *Ae. taeniorhynchus*). Other laboratory studies have shown that non-natural hosts of *A. taiwanensis*, for example, *Ochlerotarus epactius* (KnabDyar) (syn. *Ae. epactius*; see Reinert (2000), *Ochlerotatus atropalpus* (Coquillett) Munstermann and Wesson (1990) and *Ochlerotatus taeniorhynchus* (Wiedemann) (Garcia et al., 1994), are able to host this protozoon and provide it the necessary conditions to complete its life cycle. However, changes in fitness can occur, such as a decrease in wing size, life history and shortening of the pupal, among others (GARCIA et al., 1994). Comiskey et al. (1999) stated that when these protozoa infect *Ae. aegypti* they are usually unable to fully develop and can cause morbidity or kill the host. According to Reeves (2004), if mosquitoes suffer significant mortality due to gut symbionts in nature, then females might avoid water contaminated with these organisms. However, the rearing water from larvae infected with *A. taiwanensis* was more acceptable to ovipositing females than distilled water or rearing water from uninfected larvae. Earlier, Reeves and McCullough (2002) infected the Sabethine mosquito *Wyeomyia smithii* with *A. taiwanensis* and the parasite developed and invaded the Malpighian tubules in up to 70% of mosquitoes without causing any mortality. According to Comiskey et al. (1999), the negative effects of gregarines on host fitness can be exaggerated when hosts are crowded, underfed, or in competition. This may result from consumption of available resources by the parasite, or diversion of those resources for use by the host to repair damaged tissue and to elicit immune responses against the parasite.

Conclusion and Perspectives

Although most gregarines are often considered non-pathogenic to their natural hosts (HENRY, 1981), their impact on infected insects is not always clear because of a lack of knowledge about their biology and possible effects on their hosts. Laboratory studies have shown that non-natural hosts of *Ascogregarina* spp. can host these parasites, providing them with the means to complete their biological cycle. However, these parasites can negatively influence the development of the host.

It is important to remember that *Ae. albopictus* and *Ae. aegypti* can coexist in the same breeding places (FANTINATTI et al., 2007; PROPHIRO et al., 2011; LOUNIBOS et al., 2016). This behaviour could be beneficial for *Ae. albopictus* in terms of competition, if the pathogenicity of *Ascogregarina* spp. becomes more significant to the non-natural host (*Ae. Aegypti*). When the level of parasitism within a population is high, negative effects have been reported, as previously cited by the above authors. Also, when parasitism begins in the host midgut, there is possible competition for nutrition resources (CHEN, 1999; ANDREADIS, 2007). In addition, extreme variations of physiological conditions associated with parasitic infection, toxins, or trauma can cause necrosis in cells, resulting in direct damage to the plasma membrane, which kills the host (GOLSTEIN; KROEMER, 2007). Moreover, mosquito populations parasitized by *Ascogregarina* spp. demonstrated that these protozoa influence competitive interactions between species of mosquitoes. For instance, this parasite may contribute to the competitive advantage of *Ae. albopictus* compared to *Ae. triseriatus* (ALIABADI; JULIANO, 2002). Therefore, the physiological impact caused by *Ascogregarina* parasites in mosquitoes requires further research.

According to Lima-Camara (2016), over the last 10 years we have seen the emergence of several diseases transmitted by mosquitoes, especially arboviruses (e.g., dengue, chikungunya, West Nile, Mayaro and Zika viruses) in different countries of the Americas. Compared to the United States (Table 1), in South America the distribution of *Ascogregarina* species and the pathogenic potential of these species to mosquito vectors are poorly known. There are only three publications describing the occurrence of *A. taiwanensis* and *A. culicis* in natural populations of *Ae. aegypti* and *Ae. albopictus* in Argentina (VEZZANI; WISNIVESKY, 2006) and Brazil (PASSOS; TADEI, 2008; ALBICÓCCO; VEZZANI, 2009; PROPHIRO et al., 2017). Therefore, it is very important to better understand the conditions that modify prevalence and infection intensity of *Ascogregarina* spp. in mosquitoes, in order to evaluate whether these parasites can really impact the host population.

As observed, various species of *Ascogregarina* are involved in the negative effects of mosquito fitness, which can be exploited as a new biocontrol tool. However, it is important to dedicate more studies to understanding the biology of mosquitoes parasitized with these protozoa. Such studies might clarify whether some effects are related to underfed larvae, or feeding competition with sibling species (e.g., *Ae. aegypti* and *Ae. Albopictus*) in the same breeding places, and other biological aspects that could be used as possible biocontrol strategies. In addition, a protocol for the mass reproduction of *Ascogregarina* is unknown. It is necessary to know if these protozoa can be mass reproduced, and how they could be released into the environment, under what conditions and at what costs.

Even when some *Ascogregarina* species do not play an important role in the biocontrol of some mosquito populations, they have been becoming increasingly important, since they could be involved in the maintenance of arboviruses in the breeding places of mosquitoes. Moury et al. (2003) obtained vertical transmission of the chikungunya virus through the oocyst of *A. culicis* in *Ae. aegypti* mosquitoes under laboratory conditions. They suggested that these protozoa may play an important role in the maintenance of the chikungunya virus during the inter-epidemic period. Thus, it is of great importance to determine whether *A. taiwanensis* and *A. culicis* could influence the replication and maintenance of arboviruses, such as dengue and Zika viruses, and consequently influence human infection.

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