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Life cycle traits, secondary production and DNA barcode of *Oxyurella ciliata* Bergamin, 1939 (Crustacea, Branchiopoda, Anomopoda, Chydoridae)

Erika dos Santos Silva[1,3,*], Raquel Aparecida Moreira[2], Mateus Pereira da Silva[3], Tereza Cristina Orlando[3], Maria José dos Santos-Wisniewski[3] and Odete Rocha[1,4]

[1] Post Graduate Program in Ecology and Natural Resources, Universidade Federal de São Carlos, Rodovia Washington Luís, Km 235, CEP 13565-905, São Carlos, SP, Brasil.
[2] NEEA/CRHEA/SHS and PPG-SEA, Escola de Engenharia de São Carlos, Universidade de São Paulo, Av. Trabalhador São Carlense, 400, 13.560-970, São Carlos, Brazil.
[3] Institute of Nature Sciences - Universidade Federal de Alfenas, Gabriel Monteiro da Silva Street, 700, 37. 130-001, Alfenas, MG, Brasil.
[4] Department of Ecology and Evolutionary Biology, Universidade Federal de São Carlos. Rodovia Washington Luis, km 235, 13.565-905, São Carlos, SP, Brazil.

[*] Corresponding author: erika_2990@hotmail.com

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ABSTRACT

Wife cycle traits, secondary production and DNA barcode of *Oxyurella ciliata* Bergamin, 1939 (Crustacea, Branchiopoda, Anomopoda, Chydoridae)

This study the life cycle and quantify the secondary production of the cladoceran *Oxyurella ciliata* under controlled conditions in a laboratory and use molecular biology as a tool to investigate its genetic characteristics. The organisms were collected from Baia do Gerente, a pond from the Pantanal region, MS state, Brazil. They were acclimatized, maintained at a controlled temperature (25 ± 1 °C) and photoperiod (12/12h light-dark), fed with the microalgae *Raphidocelis subcapitata* and observed daily to obtain the data. *O. ciliata* had a high total egg production of 34.18 ± 9.68 eggs/female and an average longevity of 58.50 ± 16.30 days. These values differed from those previously reported for *O. longicaudis*, another congeneric species. There was an exponential growth of biomass until instar 6 and the largest secondary production was from the young to the adult phase, which corresponds to the beginning of the reproductive phase. The molecular data revealed that the genetic divergence between the sequence of *O. ciliata* and that of *O. longicaudis* is approximately 18 %, which seems high considering that both belong to the same genus. Comparing life cycle data and DNA *Barcode*, *Oxyurella ciliata* and *O. longicaudis* are very distant and have distinct morphological and biological characteristics, such as: body size, egg size, growth, fertility, longevity and development times. This study highlights the importance of molecular studies and information on the life cycle of neotropical cladocerans, in an integrated way, to have a better taxonomic and ecological interpretation of the species.

Key words: zooplankton, biology, molecular analysis, COI, cladocera taxonomy

RESUMO

Traços do ciclo de vida, produção secundária e DNA barcode de* Oxyurella ciliata *Bergamin, 1939 (Crustacea, Branchiopoda, Anomopoda, Chydoridae)

Este estudo teve como objetivo conhecer o ciclo de vida e quantificar a produção secundária do cladócero Oxyurella ciliata *sob condições controladas em laboratório e utilizar a biologia molecular como ferramenta para investigar suas características genéticas. Os organismos foram coletados na Baia do Gerente, uma lagoa da região do Pantanal, estado do Mato Grosso do Sul, Brasil. Os cladóceros foram aclimatados, mantidos em temperatura controlada (25 ± 1 °C) e fotoperíodo (12/12h claro-escuro), alimentados com a microalga* Raphidocelis subcapitata *e observados diariamente para obtenção dos*

dados. A espécie O. ciliata *apresentou alta produção total de ovos de 34.18 ± 9,68 ovos/fêmea e longevidade média de 58.50 ± 16.30 dias. Esses valores diferiram dos relatados anteriormente para* O. longicaudis*, outra espécie congenérica. Houve um crescimento exponencial da biomassa até o ínstar 6 e a maior produção secundária obtida foi da fase jovem para a fase adulta, que corresponde ao início da fase reprodutiva. Os dados moleculares revelaram que a divergência genética entre a sequência de* O. ciliata *e a de* O. longicaudis *é de aproximadamente 18 %, o que parece alto considerando que ambos pertencem ao mesmo gênero. Comparando dados de ciclo de vida e código de barras de DNA,* Oxyurella ciliata *e* O. longicaudis *são muito distantes e possuem características morfológicas e biológicas distintas, tais como: tamanho corporal, tamanho do ovo, crescimento, fertilidade, longevidade e tempos de desenvolvimento. Este estudo destaca a importância da ampliação de estudos moleculares e informações sobre o ciclo de vida dos cladóceros neotropicais, de forma integrada, para uma melhor interpretação taxonômica e ecológica das espécies.*

Palavras chave: *zooplâncton, biologia, análise molecular, COI, taxonomia de cladóceros*

INTRODUCTION

Neotropical cladocerans from Chydoridae family have a worldwide pattern of high species diversity, especially in water bodies with abundant aquatic macrophyte vegetation (Frey, 1980; Elmoor-Loureiro, 2016). Chydorids comprise approximately 47 % of currently known species of Cladocera group (Forró et al., 2008). As most microcrustaceans, they are important links in food chains whether acting as herbivores, as prey in aquatic trophic chains or nutrient recyclers, as detritivore feeders (Sterner, 2009; Elmoor-Loureiro, 2016; Cortez-Silva et al., 2022).

Classic taxonomy and geographic distribution of Cladocera in general date from nineteen century throughout the Americas, but only only recently (last fifty years) changed to be devoted to studies on life cycle, particularly the reproductive parameters of species and recently intensified to explore the genetic material (Silva et al., 2014; Castilho et al., 2015; Abreu et al., 2021).

Knowledge on ecological, genetic and bionomical aspects of species is essential to understand the dynamics of populations, as well as their role and function in communities and ecosystems (Hébert et al., 2016; Braghin et al., 2018). Studies on the life history of cladocerans can provide relevant data for functional diversity and ecotoxicological studies (Barnett et al., 2007; Castilho et al., 2012). Similarly, biomass quantification studies and secondary production of aquatic populations and communities provide information on the organic matter available at different trophic levels and can characterize the complexity of the main biotic interactions, such as competition, predation and natural disturbances (Echevarría et al., 1990; Ahrens & Peter, 1991). Cultivation under controlled conditions allows a detailed observation of individuals' development and a better understanding of several bionomical aspects, such as body growth, reproduction and longevity (Silva et al., 2014). These data can be used to select species to be used as test organisms or as indicators in environmental quality studies, thus contributing to the management and preservation of aquatic environments (Adema, 1978; Freitas & Rocha, 2006; Mansano et al., 2018).

Several studies on the molecular biology of zooplanktonic organisms, including cladocerans, have been carried out (Makino et al., 2017, 2020; Moreno et al., 2017; Elías-Gutiérrez et al., 2018; Montoliu-Elena et al., 2019; Abreu et al., 2021). In Brazil, only two studies with COI sequences of the Cladocera species belonging to the Chydoridae family had the life cycle study carried out simultaneously with that of molecular biology, those of *Flavalona margipluma* (Silva et al., 2014) and *Oxyurella longicaudis* (Castilho et al., 2015). Studies based on this gene contribute to taxonomic identification, generating informative data for the study of the phylogeny of species (Adamowicz et al., 2004; Elías-Gutiérrez et al., 2018; Yamamoto et al., 2020). They can still assist in identifying inva-

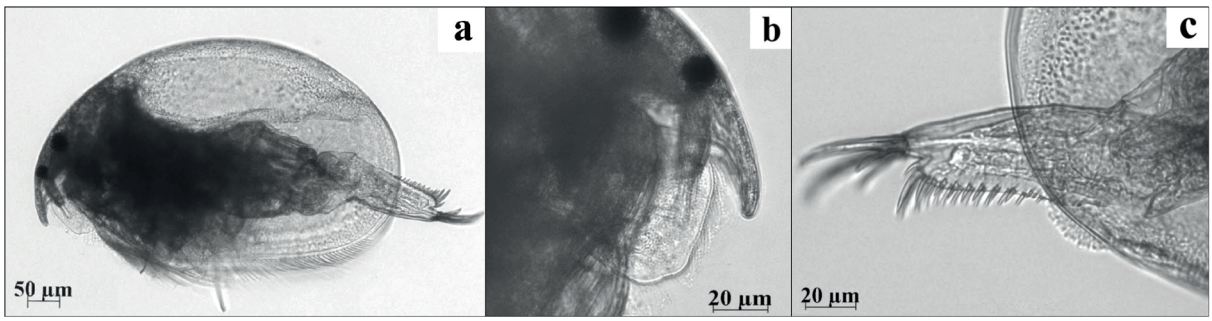

Figure 1. *Oxyurella ciliata* (Crustacea: Anomopoda; Chydoridae): A - General view , B - Rostrum developed and labral keel , C - Post-abdomen. Oxyurella ciliata *(Crustacea: Anomopoda; Chydoridae): A - Visão geral, B - Rostro desenvolvido e quilha labral, C - Pós-abdômen.*

sive and cryptic species, in addition to providing information on the geographic distribution of specific taxa (Valentini et al., 2009; Jeffery et al., 2011). In addition, molecular studies contribute to relocating some species of the Chydoridae family, such as those of the *pulchella*-group and *Ovalona* (Abreu et al., 2021)

In this context, in the present study, we aimed to investigate the life history, quantify the biomass and secondary production and genetic identity of the chydorid *Oxyurella ciliata*. The genus *Oxyurella*, belonging to the subfamily Aloninae, and has of seven species described, with a species inquirenda (Kotov et al., 2013). In Brazil, there are records of two species of *Oxyurella*: O. longicaudis and *O. ciliata* (Sousa & Elmoor-Loureiro, 2019). The species *O. ciliata* Bergamin, 1939 (Crustacea, Branchiopoda, Anomopoda, Chydoridae), has a wide geographical distribution occurring on the American (Elias-Gutiérrez et al., 2006) and African continents (Egborge et al., 1994; Imoobe, 2011). So far, it has been found in North America, in Mexico (Elías-Gutiérrez et al., 2006), in Central America, in Guatemala (Van De Velde et al., 1978), Haiti (Collado et al., 1984) and the Dominican Republic (Acosta-Mercado et al., 2012) and in South America, in Venezuela (Rey & Vázquez, 1986; Zoppi De Roa & Vasquez, 1991; Zoppi De Roa & López, 2008), Colombia (Fuentes-Reinés & Roa, 2013; Fuentes-Reinés, 2014) and Brazil (Rocha et al., 2011; Santos-Wisniewski et al., 2011; Sousa & Elmoor-Loureiro, 2012).

MATERIALS AND METHODS

Stock cultures and maintenance of *Oxyurella ciliata*

Specimens of *Oxyurella ciliata* were collected from Baia do Gerente, Aquidauana municipality (19° 22’ 16’’ S 56° 21’ 02’’ W). Sampling was made with a plankton net (68 µm mesh opening) by horizontal trawls, in the littoral region among macrophytes. This freshwater pond had abundant macrophytes, mostly *Eichhornia crassipes* (personal communication). The species *O. ciliata* has an oval body and carapace with rounded posterior angles. The keel of the labrum is wide and rounded, with setae on the anterior margin. The posabdomen is slightly tapered distally and has lateral spicules, in addition to 15-16 anal denticles, the distal 2-3 being larger than the others. The claw has a basal spine, located some distance from the base of the claw.

Parthenogenetic females of *Oxyurella ciliata* (Fig. 1 A-C) were isolated, transferred and cultured in 1 L beakers containing reconstituted water, and maintained at controlled temperature and photoperiod (25 ± 1 °C and 12/12h light-dark cycle) in the Limnology laboratory at the Federal University of São Carlos. Physical and chemical conditions of the culture medium were: 40 to 48 mg/L CaCO3 hardness and ≈ 7.0 pH. Organisms were fed daily on microalgae *Raphidocelis subcapitata* Korschikov cultured in CHU 12 (Chu, 1942) medium and harvested at exponential growth phase.

They were provided a suspension of10^5 cells/L supplemented with a mixed food suspension (1 mL/L), containing biological yeast and fermented fish feed (Tetramim brand). Half culture medium was renewed every two days (ABNT, 2017).

Embryonic and post-embryonic development

After acclimatizing the species in the laboratory for 10 generations, 15 ovigerous females at the third brood were isolated for the life cycle experiment. Thirty neonates aged less than 24 hours were isolated, measured, and kept individually in non-toxic polypropylene plastic small vessels containing 25 mL of reconstituted water, under the same conditions previously described for parental females. During the first twenty days, observations were made three times per day to determine embryonic and post-embryonic development times until primipara instar (first egg production).

From there, observations were made once a day to obtain data on fertility, neonate production and longevity. Body sizes were measured daily under an optical microscope using a 40× magnification to determine individual growth. The number of eggs produced was counted and the size of eggs measured used for biovolume and biomass calculations.

Biomass calculation and secondary production

Individual biomass calculations were performed using a linear regression that relates length (mm) to dry weight (µg) (Bottrell et al., 1976). Biomass (W) was calculated for each instar using body size values measured along the life cycle. The linear regression equation was used, which relates length (mm) to dry weight (µg): LnW = Ln(a) + b Ln(L), where a and b are constants obtained from the regression model between weight and length and L is length (mm). For the determination of secondary production, daily increment in biomass method (Winberg et al., 1965) was used and applied to each individual. In addition to the total secondary production, the production of the neonate to the young stage, the production of young to adult internship, the production of total body growth and total reproductive production (eggs) were calculated using the mean of the values obtained from the individuals.

To adjust the body growth curves throughout the life cycle and weight-length relationships, the OriginPro version 8 program was used.

DNA barcode

For the DNA *Barcode* analysis, 224 specimens from the laboratory culture were fixed in ice cold absolute ethanol (Merck). Genomic DNA was extracted using the alkaline lysis method using the HotSHOT protocol (Montero-Pau et al., 2008). For amplification of the COI region, ZplankF1 and ZplankR1 primers (Prosser et al., 2013) were used. The PCR reactions had a total volume of 25 µl and were performed according to Ivanova et al. (2006) using Platinum *Taq* (Invitrogen, Carlsbad, CA, USA) as an enzyme. The PCR conditions were: 95 °C for 3 minutes as initial denaturation and 40 cycles of 95 °C for 45 seconds, 45 °C for 45 s and 72 °C for 1 minute, followed by 72 °C for 10 minutes. The PCR products were sequenced bidirectionally after treatment with the Exo-SAP enzymes (Fermentas) and applied to a 3130xl Genetic Analyzer sequencer (Life Technologies, Carlsbad/CA/USA) following the manufacturer's instructions.

The COI sequences of *Oxyurella ciliata* were aligned in the MEGA 7 software (Kumar et al. 2016) with other COI sequences that showed great similarity when compared to the BLAST tool of Genbank (https://blast.ncbi.nlm.nih.gov/Blast.cgi). All COI sequences of the genus *Oxyurella* were used for the analysis. The genetic divergences were based on the limits established by Hebert et al. (2003). The 2-parameter Kimura distance model (K2P) was used to calculate genetic divergences and the analysis was performed using MEGA 7 (Kumar et al., 2016) with Neighbor Joining (NJ) and non-parametric bootstrapping of 1000 replicates.

RESULTS

Life cycle

The maximum size reached by an adult was 540.0 µm and the average adult size was 518.18 ± 10.79 with an average age of 29.73 ± 17.56

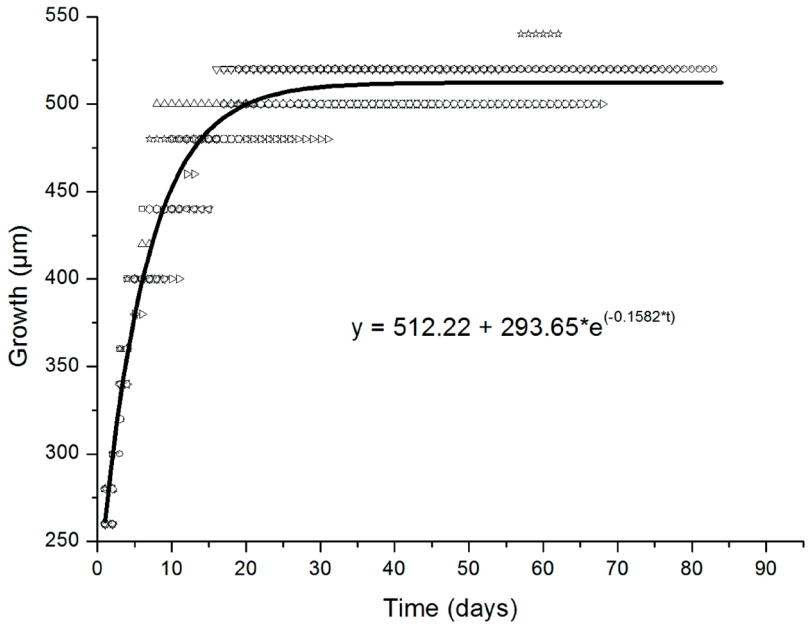

Figure 2. Mean individual growth curve adjusted by the von Bertalanffy model for *Oxyurella ciliata* (Cladocera, Chydoridae). Grown in the laboratory at controlled temperature conditions at 25 ± 1 °C and 12h light/12h dark photoperiod (n = 11). *Curva de crescimento médio individual ajustada pelo modelo de von Bertalanffy para* Oxyurella ciliata *(Cladocera, Chydoridae). Espécies cultivadas em laboratório em condições controladas de temperatura a 25 ± 1 °C e fotoperíodo de 12h claro/12h escuro (n = 11)*

days. The neonates (n = 11) had an average size of 281.25 ± 15.0 µm with less than 24 h of age and reached an average size (n = 11) of 396.0 ± 13.0 µm in the first egg laying. During the entire life cycle, 9 instars in total were recorded. There were four pre-reproductive instars between the newborn neonate and the primipara female. Ecdysis between the neonate and juvenile stages occurred quickly, between one and two days.

Oxyurella ciliata reached maturity at 3.78 ± 0.71 days. The average fecundity of females was 1.86 ± 0.35 eggs/female/brood (n = 11), producing an average of 34.18 ± 9.68 eggs/female throughout the life cycle. The fertility of the females in the first laying and close to senescence was always that of an egg per female per brood. The species had maximum longevity of 84 days and average longevity of 58.5 ± 16.3 days. The embryonic development time was 1.99 ± 0.06 days.

The growth of species was exponential until the twentieth day of life, reaching the asymptotic value after this period, when a smaller and slower body growth of the species was observed (Fig. 2).

Regarding biomass for each instar, there was an exponential growth in dry weight up to instar 6, but in the last three instars, the weight remained approximately constant (Fig. 3). On instar 4, which corresponds to the beginning of the reproductive age, there was no variation in dry weight between individuals and sexual maturity occurred when the organisms reached an average dry weight of 0.5 µg. A greater variation in weight was observed among individuals in adulthood (instars 7 and 8).

There was less secondary production in the neonatal to young stages and higher production from the young to the adult stage, which corresponds to the beginning of the reproductive phase (Fig. 4). The total secondary production was higher when compared to the reproductive and body growth. The value of secondary reproductive production (eggs) was close to that of total growth.

DNA barcode

The sequencing of the COI region of *O. ciliata* re-

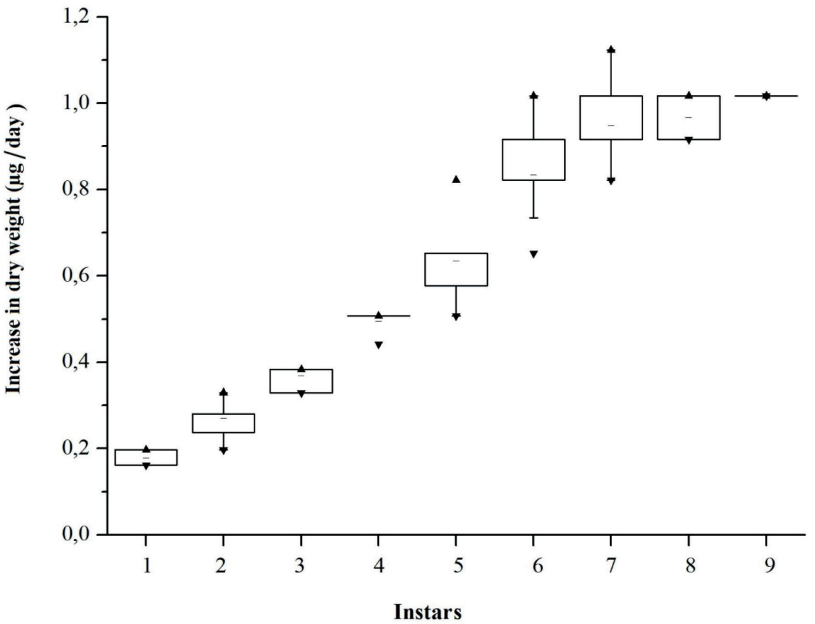

Figure 3. Variation of instantaneous biomass (dry weight in µg) for each instar of *Oxyurella ciliata* (Cladocera, Chydoridae), in laboratory cultivation at 25 ± 1°C and photoperiod of 12h light/12h dark photoperiod (n = 11). *Variação da biomassa instantânea (peso seco em µg) para cada instar de* Oxyurella ciliata *(Cladocera, Chydoridae), em cultivo em laboratório a 25 ± 1°C e fotoperíodo de 12 h-claro/12 h-escuro (n = 11).*

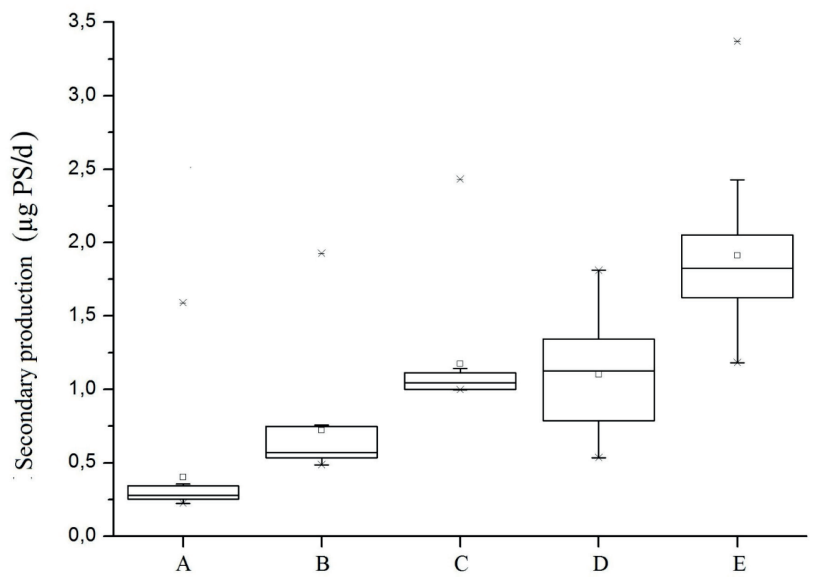

Figure 4. Secondary production (µg PS day-1) for the species *Oxyurella ciliata* (Cladocera, Chydoridae), grown in the laboratory at 25 ± 1°C and photoperiod of 12 h-light/12 h-dark (n = 11). A = production of the stage from neonate to youth; B = production of the youth to the adult internship; C = production of total body growth; D = total reproductive production (eggs); E = Total secondary production. *Produção secundária (µg PS dia-1) para a espécie* Oxyurella ciliata *(Cladocera, Chydoridae), cultivada em laboratório a 25 ± 1°C e fotoperíodo de 12 h-claro/12 h-escuro (n = 11). A = produção do estágio de neonato ao jovem; B = produção do estágio de jovem ao adulto; C = produção do crescimento corporal total; D = produção reprodutiva total (ovos); E = Produção secundária total.*

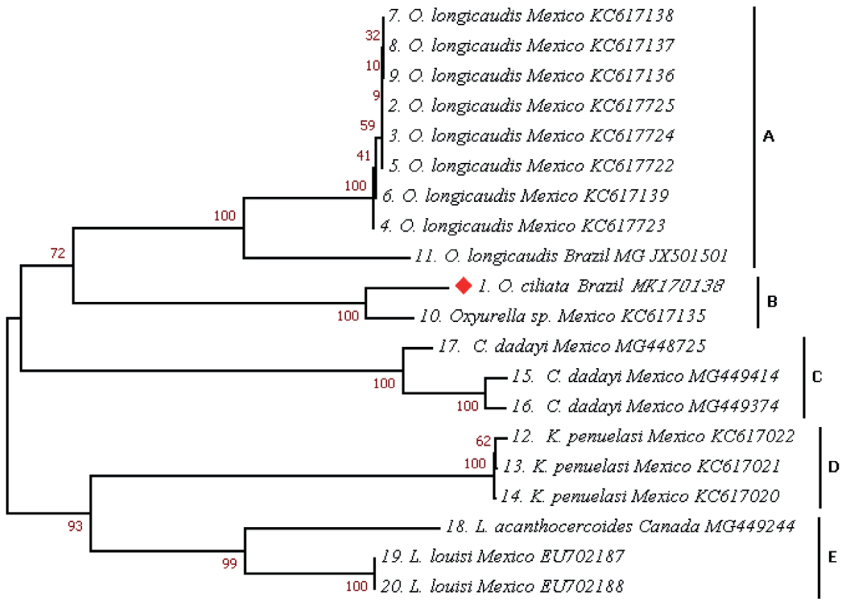

Figure 5. Neighbor-Joining tree representing the genetic proximity of *Oxyurella ciliata* (Cladocera, Chydoridae) with other species of Chydoridae. The numbers on each node correspond to the percentages of the bootstrapping support (1000 replicates). Distances were calculated using the Kimura 2-parameter method (K2P) and the bar indicates the number of substitutions per site. The GenBank accession number and locations are inserted after the name of each species. ♦ = espécie do presente estudo; O = Oxyurella; C = Camptocercus, K = Karualona, L. = Leydigia. *A árvore filogenética Neighbor-Joining representa a proximidade genética de* Oxyurella ciliata *(Cladocera, Chydoridae) com outras espécies de Chydoridae. Os números em cada nó correspondem às porcentagens do teste de bootstrap (1000 réplicas). As distâncias foram calculadas usando o método de 2 parâmetros de Kimura (K2P) e a barra indica o número de substituições por sítio. O número de acesso e as localizações do GenBank são inseridos após o nome de cada espécie. ♦ = espécie do presente estudo; O = Oxyurella; C = Camptocercus, K = Karualona, L. = Leydigia.*

Table 1. K2P genetic divergence among COI sequences of *Oxyurella ciliata* (Cladocera, Chydoridae) from Brazil and other species of Chydoridae from the GenBank database. The GenBank access number is found after the name of each specimen. O = Oxyurella; K = Karualona, C = Camptocercus, L. = Leydigia. *Divergência genética de K2P entre sequências COI de* Oxyurella ciliata *(Cladocera, Chydoridae) do Brasil e outras espécies de Chydoridae do banco de dados GenBank. O número de acesso do GenBank é encontrado após o nome de cada espécime. O = Oxyurella; K = Karualona, C = Camptocercus, L. = Leydigia.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1. *O. ciliata* Brazil: MK170138																			
2. O. *longicaudis* Mexico KC617725	0.181																		
3. *O. longicaudis* Mexico KC617724	0.181	0.000																	
4. *O. longicaudis* Mexico KC617723	0.179	0.002	0.002																
5. *O. longicaudis* Mexico KC617722	0.181	0.000	0.000	0.002															
6. *O. longicaudis* Mexico KC617139	0.183	0.002	0.002	0.000	0.002														
7. *O. longicaudis* Mexico KC617138	0.187	0.000	0.000	0.002	0.000	0.002													
8. *O. longicaudis* Mexico KC617137	0.181	0.000	0.000	0.002	0.000	0.002	0.000												
9. *O. longicaudis* Mexico KC617136	0.185	0.000	0.000	0.002	0.000	0.002	0.000	0.000											
10. *Oxyurella* sp. Mexico KC617135	0.034	0.166	0.166	0.164	0.166	0.166	0.168	0.160	0.167										
11. *O. longicaudis* Brasil MG JX501501	0.181	0.080	0.080	0.078	0.080	0.076	0.076	0.083	0.080	0.186									
12. *K. penuelasi* Mexico KC617022	0.253	0.227	0.227	0.224	0.227	0.219	0.222	0.237	0.223	0.261	0.231								
13. *K. penuelasi* Mexico KC617021	0.254	0.223	0..223	0..220	0.223	0.218	0.221	0.237	0.218	0.262	0.226	0.003							
14. *K. penuelasi* Mexico KC617020	0.255	0.223	0.223	0.220	0.223	0.218	0.221	0.237	0.219	0.263	0.227	0.003	0.002						
15. *C. dadayi* Mexico MG449414	0.215	0.219	0.219	0.216	0.219	0.231	0.234	0.222	0.225	0.220	0.222	0.265	0.260	0.255					
16. *C. dadayi* Mexico MG449374	0.210	0.219	0.219	0.216	0.219	0.231	0.234	0.222	0.225	0.215	0.222	0.271	0.266	0.261	0.011				
17. *C. dadayi* Mexico MG448725	0.210	0.199	0.199	0.197	0.199	0.209	0.215	0.204	0.205	0.215	0.202	0.243	0.239	0.234	0.036	0.034			
18. *L. acanthocercoides* Canada MG449244	0.222	0.210	0.210	0.208	0.210	0.207	0.215	0.228	0.208	0.212	0.226	0.191	0.188	0.186	0.240	0.237	0.218		
19. *L. louisi* Mexico EU702187	0.215	0.187	0.187	0.185	0.187	0.185	0.192	0.199	0.184	0.219	0.217	0.193	0.192	0.190	0.237	0.235	0.204	0.085	
20. *L. louisi* Mexico EU702188	0.215	0.187	0.187	0.185	0.187	0.185	0.192	0.199	0.184	0.219	0.217	0.193	0.192	0.190	0.237	0.235	0.204	0.085	0.000

sulted in 658 bp and the composition of bases was as follows: A = 23.4 % T = 42 % C = 13.7 % G = 20.9 and the calculated content of A-T was 65.4 %.

A genetic divergence ranging from 17.9 % to 18.5 % was found between the COI sequence of *O. ciliata* and the sequences of *O. longicaudis*, also isolated in Brazil, including the Brazilian specimen (JX501501). The divergences were also high for other Chydoridae, such as *Karualona penuelasi*, *Camptocercus dadayi*, *Leydigia acanthocercoides* and *Leydigia louisi*, which remained between 21 % and 25.5 % (Table 1). The divergence between *O. ciliata* and *Oxyurella* sp. from Mexico was 3.4 %; the lowest among all those analyzed. This result can be observed in the Neighbor-Joining tree, which shows the proximity relationship between these two sequences with a 100 % bootstrap between *Oxyurella* sp. from Mexico and *O. ciliata* from Brazil (Fig. 5).

The 20 sequences analyzed were grouped considering the genetic proximity between them. Our analysis found 5 different groups that were identified with capital letters from A to E (Fig. 5). In group A, the *Oxyurella longicaudis* species from Brazil and Mexico were grouped, while in group B the species *O. ciliata* (present study) and *Oxyurella* sp. Were grouped from Mexico.

DISCUSSION

The maximum size of adult females of *Oxyurella ciliata* has been reported to vary between 350 to 440 µm (Smirnov, 1974; Fuentes-Reines & Roa, 2013). However, in the present study, this species reached a maximum size of 540 µm and mean size of 518.18 ± 10.79, much larger than that previously reported by these authors. It is possible that in cultivation, under optimal feeding conditions, the size obtained is the maximum potential size of this species. The species of the subfamily Aloninae are larger, ranging from 350 to 1050 µm, when compared to those of the subfamily Chydorinae, which vary from 270 to 600 µm (Smirnov, 1974). The body size values of *O. ciliata* are within the range established for Chydoridae species. Body size to cladocerans have a central role in understanding biological interactions in planktonic communities, being, therefore, an important physiological and ecological attribute (Hart & Bychek, 2011).

The average sizes for the neonate (281.25 ± 15 µm) and the primipara (396 ± 13 µm) of *O. ciliata* were similar to those recorded for *Flavalona margipluma*, 288.2 ± 19.36 and 413.08 ± 28.53 µm (Silva et al., 2014), but smaller than those found for *Oxyurella longicaudis*, 503.85 ± 52.77 and 654.61 ± 45.09 µm (Castilho et al., 2015), a species belonging to the same genus as of the present study. In general, the sizes observed for *O. ciliata* were smaller than those found for the *O. longicaudis* species (Castilho et al., 2015), even though they are species of the same genus.

Throughout the life cycle, *O. ciliata* had nine instars, a number lower than that normally found for other chydorids (Table 2), such as for *Chydorus pubescens* (Santos-Wisniewski et al., 2006), *Coronatella rectangula* (Viti et al., 2013), *Leydigia acanthocercoides* (Murugan & Job, 1982) and *Alonella excisa* (Sharma & Sharma, 1998). The number of instars of *O. ciliata* recorded in the present study was close to 8.92 ± 1.23 instars, verified for *O. longicaudis* (Castilho et al., 2015). Several factors can affect the development and reproduction of Cladocera species. Among them, temperature and food have long been recognized as the most important factors (Winberg, 1971; Rocha, 1983; Hardy & Duncan, 1994; Masclaux & Richoux, 2017). Generally, the temperature has an inverse relationship with embryonic and post-embryonic development times; the higher the temperature, the shorter the development times of the organisms (Bottrell, 1975; Melão & Rocha, 2006).

The average (58.5 ± 16.3 days) and maximum (84 days) longevity found in this study for *O. ciliata* were, in general, greater than those of other species of Chydoridae with the exception of *Alonella excisa*, whose average longevity was 73.4 days (Sharma & Sharma, 1998) and *Pleuroxus denticulatus* with a maximum longevity of 121 days (Shan, 1969). Chydoridae species have a longer life cycle than species from other families of Cladocera up to 94 days (Smirnov, 1974). However, Lynch (1980) reported a smaller variation range for the Chydoridae's longevity, from 24 to 42 days. Therefore, *O. ciliata* longevity fits better in the range established by Smirnov (1974).

Regarding the primipara age, the species *O.*

ciliata reached maturity in 3.78 ± 0.71 days. The mean age of the primipara *O. ciliata* was close to that of *Alona affinis* (3.89 ± 0.32 days) and *Eurycercus lamellatus* (3.86 ± 0.24 days) at a temperature of 20 ºC (Bottrell, 1975) and at *Acroperus harpae* (3.76 days) at a temperature of 20 ºC (Melão, 1999). However, it was less than that observed for the species *O. longicaudis* (5.20 ± 0.69 days) at a temperature of 23 ºC (Castilho et al., 2015) (Table 2). This difference could be related to the temperature differences used in the experiments. On average, Chydoridae species reach maturity around six days (Lynch, 1980).

Oxyurella ciliata had average fertility of 1.86 ± 0.35 eggs per female per brood, similarly to that found by other authors for several species of the Chydoridae family (Melão, 1999; Viti et al., 2013). The size of the brood and the total fecundity of the species is different between the families of Cladocera (Sharma & Sharma, 1998). Species belonging to other families can produce more eggs per brood. For example, females of *Pseudosida ramosa*, from the Sididae family, produced about 3.4 eggs per brood cultivated at 25 °C (Freitas & Rocha, 2006). Species of the Daphniidae family, such as *Scapholeberis armata*, can produce up to 8 eggs per brood (Castilho et al., 2012), while *Ceriodaphnia silvestrii* pro-

Table 2. Comparison of the main parameters of the life cycle of *Oxyurella ciliata* (present study) with that of other cladoceran species of the family Chydoridaeand Eurycercidae. *Comparação dos principais parâmetros do ciclo de vida de* Oxyurella ciliata *(presente estudo) com outras espécies de cladóceros da família Chydoridae e Eurycercidae.*

Species	Authors	1	2	3	4	5	6	7
Aloninae								
Acroperus harpae	Bottrell (1975)	20	3.29 ± 0.24	-	15.42 ± 0.99	29	10	2.33 ± 0.2
Acroperus harpae	Melão (1999)	20	3.76	-	-	-	-	1.98
Acroperus harpae	Melão (1999)	25	3.7	-	-	-	-	1.56
Alona affinis	Bottrell (1975)	20	3.89 ± 0.32	-	16.95 ± 0.90	37	10	2.67 ± 0.22
Coronatella rectangula	Viti et al. (2013)	23.6	2.48±0.45	27.8 ± 9	28.04 ± 9.3	46	12	1.68 ± 0.13
Euryalona orientalis	Venkataraman (1990)	28 a 30	3.92	20	24	-	13	-
Flavalona margipluma	Silva et al. (2014)	25	3.24 ± 0.69	47.58 ± 6.27	46 ± 5.96	54	8	1.79 ± 0.23
Leydigia acanthocercoides	Murugan & Job (1982)	28 a 30	3	20	23	-	16	-
Leydigia ciliata	Venkataraman (1990)	28 a 30	2.62	50	46	-	28	-
Leydigia leydigi	Robertson (1988)	19	6.8	-	21	27	7.2	2.8 ± 0.105
Leydigia louisi	Martínez-Jerónimo & Gómez-Díaz (2011)	25 Cs	7.7	6.6	26.84 ± 0.75	28.5	-	-
Leydigia louisi	Martínez-Jerónimo & Gómez-Díaz (2011)	25 As	8.8	18.5	32.34 ± 2.21	39.6	-	-
Oxyurella ciliata	Present study	25	3.78 ± 0.71	34.18 ± 9.68	58.5 ± 16.3	84	9	1.99 ± 0.06
Oxyurella longicaudis	Castilho et al. (2015)	23	5.20 ± 0.69	22.55 ± 3.98	46.96 ± 9	58	8.92 ± 1,23	2.30 ± 0.5
Chydorinae								
Alonella excisa	Sharma & Sharma (1998)	19 a 23	3.17	46	73.4	-	28	-
Chydorus dentifer	Melão (1999)	20	6.44	-	-	-	-	2.66
Chydorus dentifer	Melão (1999)	25	5.73	-	-	-	-	2.2
Chydorus pubescens	Santos-Wisniewski et al. (2006)	23.6	2.37±0.43	22.3 ± 5.1	25.4 ± 4.6	31	13	1.96 ± 0.18
Chydorus sphaericus	Bottrell (1975)	20	2.93 ± 0.15	-	8.94 ± 0.15	24	9	2.11 ± 0.08
Disparalona rostrata	Robertson (1988)	19	8	-	30	37	7.2	4.8 ± 0.274
Pleuroxus denticulatus	Shan (1969)	15	4	-	-	121	-	1.25
Pleuroxus denticulatus	Shan (1969)	25	-	-	-	24	-	-
Pleuroxus uncinatus	Bottrell (1975)	20	3.3 ± 0.31	-	13.60 ± 0.24	31	11	2.2 ± 0.19
Eurycercidae								
Eurycercus lamellatus	Bottrell (1975)	20	3.86 ± 0.24	-	19.08 ± 0.73	42	13	2.39 ± 0.17
Graptoleberis testudinaria	Bottrell (1975)	20	3.33 ±0.24	-	9.48 ± 0.23	23	8	2.14 ± 0.16
Daphniidae								
Scapholeberis armata	Castilho et al. (2012)	23 ± 0.5	5.86 ± 1	47.58 ± 6.27	23 ± 4	31	7 ± 0.69	1.9 ± 0.37
Ceriodaphnia cornuta	Melão (1999)	20	4.76		9.8			3.24
Sididae								
Pseudosida ramosa	Freitas & Rocha (2006)	25 ± 0.5	6.67 ± 1.37	38.8 ± 26.36	37.1 ± 6.27			2.08
Pseudosida ramosa	Freitas & Rocha (2006)	30 ± 0.5	4.5 ± 0.54	27.8 ± 8.11	14.8 ± 1.17			1.38
Simocephalus serrulatus	Melão (1999)	20	5.18		13.4			2.58

1 - Temperature (° C); 2 - Age of the primipara (days); 3 - Average number of eggs throughout the life cycle (eggs per female); 4 - Average longevity (days); 5 - Maximum longevity (days); 6 - Total number of instars; 7 - Embryonic development (days); Cs - Commercial substrate; As - Artificial substrate.

duces an average of 9 eggs per brood (Fonseca & Rocha, 2004). Species of the Chydoridae family produce no more than two eggs per brood due to their morphology characterized by a flattened body and a small incubator chamber (Smirnov, 1974; Elmoor-Loureiro, 2016).

The reproductive performance of a species is an integrated response resulting from many metabolic processes and affected by multiple factors. In addition to these factors, one must also consider those inherent to each species, such as the body size, the maximum number and size of the eggs (Munro & White, 1975; Melão, 1999). Larger species tend to produce larger eggs, with longer development times (Smirnov, 1996). In the present study, *O. ciliata* was fed with microalgae and a mixed suspension of fish food and biological yeast. It is likely that the high longevity and greater production of eggs of this species, when compared to others (Table 2), are also related to the variety and, therefore, to the better quality of the food provided to this cladoceran during the experiment. Similarly, the type of seaweed and yeast supplementation were important factors in the characteristics of the life cycle and especially in the production of *Leydigia louisi* eggs (Martínez-Jerónimo & Gómez-Díaz, 2010).

During the entire life cycle, the *O. ciliata* species produced an average of 34.18 ± 9.68 eggs per female, a high total fertility compared to that of other species (Table 2), such as, for example, *O. longicaudis*, which produced 22.55 ± 3.98 eggs per female throughout the fertile phase of their life cycle (Castilho et al., 2015). In this specific case, it can be considered that *O. ciliata*, having greater mean longevity (58 days), had more time to invest in egg production than *O. longicaudis* with a mean longevity of 47 days. Another example reinforcing this hypothesis is that of *Alonella excisa* with greater average longevity, of 74 days, and greater total fecundity, of 46 eggs per female (Sharma & Sharma, 1998).

The embryonic development time of *O. ciliata*, 1.99 ± 0.06 days at 25 °C was similar to that of *Chydorus pubescens*, 1.96 ± 0.18 at 23.6 °C (Santos -Wisniewski et al., 2006), but less than that of *C. dentifer*, of 2.66 days at a lower temperature, of 20 °C (Melão, 1999), which suggests that if grown at the same temperature, the development times for both could be very close (Table 2). Higher temperatures correspond to shorter development times and may, for example, double the metabolic rate with an increase of 10 ºC in the temperature of the environment (Winberg, 1971; Bottrell, 1975). Another factor that can contribute to differences observed in the duration of species development, is the size of the species and the eggs themselves (Smirnov, 1996).

Oxyurella ciliata showed an increase in biomass up to the reproductive phase, with great weight gain in the first instars. The *Ceriodaphnia silvestrii* species also had greater growth in the first instars (Fonseca & Rocha, 2004). There was also greater secondary production in the youth to the adult stage, which includes, in addition to the production invested in body growth, the biomass invested in egg production. Some species of Cladocera invest more energy in the initial period of the life cycle, quickly reaching the maximum size and from there, throughout the life cycle, the assimilated matter/energy reserves are allocated in reproduction (Lynch, 1980; Hartneet, 2019). This was observed for the *O. ciliata* species, as the reproductive production was higher when compared to the secondary production of the stages from neonate to young and from young to adult. Therefore, in the reproductive phase, the species allocated more energy for egg production.

In the present study, the first COI sequence for *O. ciliata* was determined. Regarding the DNA barcode, the percentage of A-T (65.4 %) was similar to that registered by other authors for COI of Chydoridae (60 %) (Sacherová & Hebert, 2003; Belyaeva and Taylor 2009). This percentage was also close to that found for the *O. longicaudis* species from Brazil (64.4 %) (Castilho et al., 2015).

The differences between the sequences of individuals of the same species cannot exceed 3 % (Hebert et al., 2003). Other authors cite similar rates of divergence, such as Jeffery et al. (2011), who proposes a reevaluation in the taxon when divergences are between 3 % and 5 % and that in the case of divergences greater than this value, the species are considered different taxa. Divergence values greater than 3 % were predicted since there are no other O. ciliata sequences in the database. However, the divergences found were much higher than this intraspecific threshold, reaching

18.5 % for *O. longicaudis* (KC617136), a specimen belonging to the same genus.

The magnitude of the genetic divergence in relation to other species of Chydoridae was also high, such as *Karualona penuelasi*, *Camptocercus dadayi*, *Leydigia acanthocercoides* and *L. louisi* (21 % and 25.5 %). These sequences were inserted as an external group due to the phylogenetic relationship with the studied group (Sacherová & Hebert, 2003).

Group B of our analysis houses the sequence of *Oxyurella ciliata* and *Oxyurella* sp. (KC617135) from Mexico with a genetic distance of 3.4 %. These data suggest that these two taxa may belong to the same taxonomic entity since they are very close genetically. In another study, the genetic divergence between *O. longicaudis* from Brazil and the sequences of *O. longicaudis* from Mexico were also high, at 8 % (Castilho et al., 2015). Therefore, a detailed morphological analysis between specimens of these two taxa would be interesting, uma vez que *O. ciliata* presents some morphological characteristics (i.e., setulated labral keel) that readily separates this species from the rest of species of *Oxyurella*. In view of this, these authors suggested a detailed review of the morphological studies and other molecular markers to better elucidate the taxonomic status of these two entities.

CONCLUSIONS

Oxyurella ciliata and *O. longicaudis* have distinct morphological and biological characteristics, such as: body size, egg size, growth, fertility, longevity and development times. The high genetic divergence found confirms this difference and suggests that further studies on ecology and molecular biology with other markers should be carried out for species belonging to this genus. *Oxyurella ciliata* is a little-studied species and more detailed studies on its morphological characteristics are still needed. The knowledge of the molecular biology of the species of Cladocera can, therefore, help to better establish the taxonomic status for both the species already described and for new morpho-species. Moreover, information on morphology, phenotypic variations, distribution and ecology of many zooplanktonic species, which were recorded in studies with descriptions of species and their life cycle, are complementary with the molecular biology approach were considered, hence the importance of combining this knowledge, such as what was accomplished in this study.

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AUTHOR'S CONTRIBUTIONS

E.S.S. - Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft; M.P.S. - Methodology, Analysis of the Molecular Biology, Writing - Review & Editing; T.C.O. - Methodology, Analysis of the Molecular Biology, Writing - Review & Editing; R.A.M. - Methodology, Writing - Review & Editing; M.J.S.W. - Conceptualization, Methodology, Writing - Review & Editing; O.R. - Conceptualization, Resources, Methodology, Writing - Review & Editing.

Declarations

Conflict of interest: The author declared that there is no conflict of interest.

Data Availability Statement
Data, associated metadata, and calculation tools are available from the corresponding author (erika_2990@hotmail.com).

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